

A revision of the western Atlantic Ocean genus *Engina* with notes on *Hesperisternia* (Gastropoda: Buccinidae: Pisaninae)

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ABSTRACT

The western Atlantic Ocean members of the genus *Engina* Gray, 1839, are reviewed. The following taxa are recognized: *E. annae* new species, *E. corinnae* Crovo, 1974, *E. demani* de Jong and Coomans, 1988, *E. goncalvesi* Coltro, 2005, *E. itzamnai* (Watters, 2009), *E. lignea* new species, *E. permixta* new species, *E. turbinella* (Kiener, 1836), and *E. williamsae* new species. Distributional notes are also given for *Hesperisternia karinae* (Nowell-Usticke, 1959).

INTRODUCTION

The systematics of *Engina* is confusing as the genus has a complicated taxonomic history. Early species were described in the genus *Voluta* by Linnaeus (1758) and Wood (1828), in *Buccinum* by Lamarck (1822), in *Columbella* by Sowerby (1832) and Duclos (1840), and in *Purpura* by Kiener (1836). Even after the description of the genus *Engina* in 1839 species continued to be described in *Buccinum* by Küster (1858), in *Pollia* by Dunker (1860), in *Tritonidea* by E.A. Smith (1884), and other genera, but especially in *Ricinula* by Reeve (1846). In addition, aside from actual buccinid species, members of other families (Muricidae, Columbellidae, etc.) also were included in those genera and, for the simple reason that many of those small shells look similar, it was not until Pease (1860), Melvill (1893; 1894a; 1894b; 1895) and Melvill and Standen (1895) that the name *Engina* was finally used in publications. Tryon (1883) and Pace (1902) considered *Engina* to be a columbellid genus.

Engina was introduced by J.E. Gray in *The Zoology of Captain Beechey's Voyage*. In the Introduction to this publication, Beechey (in Gray, 1839: vii) stated that "I wish I could with sincerity have included with the above-mentioned [acknowledged] names that of Mr. J. E. Gray, who undertook to describe the shells, but the publication has suffered so much by delay in consequence of his having been connected with it, that it is a matter of the

greatest regret to me that I ever acceded to his offer to engage in it. . . [This eight year delay] has been occasioned entirely by Mr. Gray's failing to furnish his part in spite of every intercession from myself and others." Beechey continued in this vein for another page. Gray had listed two species in the genus, neither collected during the voyage, both new but unillustrated, and did not select a type of the genus. Both species, *E. zonata* and *E. elegans*, have been the subject of debate due not only to Gray's lack of illustration, but to his apparent gross mis-measurement of the specimens, giving lengths 10 times greater than the actual shells, and the vague type localities for both: "Atlantic Ocean." Gray subsequently (1847) picked *E. zonata* as the type while misspelling *Engina* as *Enzina* (also misspelled in 1842).

Landau and Vermeij (2012) considered *Engina* to be a group of intertidal and shallow subtidal species. However, most of the species considered here occur in significantly deeper water; live individuals often occur in depths > 45 m, some to hundreds of meters. Of the western Atlantic species only *E. turbinella* truly occurs predominately in shallow water. Most species are associated with rocky reefs or coral debris, whereas some occur in caves. As with many other gastropod genera, *Engina* harbors a number of species that are common or even abundant whereas several species are quite rare and rarely represented in collections.

The type species of *Engina*, *E. turbinella*, is a member of the shallow water fauna and therefore shows the shell characteristics that are representative of *Engina* species from that fauna. Most, or all, shallow water *Engina* species bear the characteristic radially oriented lirae on the columella that are seen in the type species. Nevertheless many *Engina* live in deeper water and differ slightly or even radically from the shallow water morphs. In deeper water (ca. > 45 m) species may lack these radially orientated lirae on the parietal part. The shallow and deep water morphs are not well separated and it remains a question of whether this is the result of variability (the opinion followed in the present paper) or rather that our current concept of *Engina* is based on a heterogeneous group (the result of the presence of unrecognized genera).

In the present paper we regard *Engina* in a rather conservative way, grouping together the shallow and deep-water species. Further study may indicate that additional genera are required.

The type species of *Engina*, together with the species discussed in the present paper, are members of the Atlantic Ocean fauna. A much larger number of *Engina* species is known from the Indo-West Pacific and eastern Pacific oceans. We believe that both the Atlantic and Indo-West Pacific species belong to the same genus, as so many other genera do, and we see no reason to split *Engina* into distinct groups based on geographical distribution.

Apart from a higher biodiversity in the Indian and Pacific oceans, the morphological variability within the genus is also higher there than in the Atlantic Ocean. Slender, fusiform shells are a frequent shape in the Indo-West Pacific Ocean whereas none are known to us from the Atlantic Ocean. Those slender species have a different appearance than do broad ones and tend to live in deeper water; nevertheless we regard them as included within the variability of the genus. "Typical" species have radiating columellar riblets. In some species those are well expressed and striking but other species show this sculpture only under magnification.

Many Western Atlantic Ocean species have eastern Pacific Ocean cognates. Atlantic taxa such as *E. turbinella* and *E. permixta* closely resemble Pacific species such as *E. mantensis* Bartsch, 1928, *E. maura* (Sowerby, 1832), and *E. tabogaensis* Bartsch, 1931. The Pacific *E. pulchra* (Reeve, 1846) is particularly close to the Atlantic *E. demani*. But taxa such as the Pacific *E. fusiformis* Stearns, 1894, and the Atlantic *E. goncalvesi* do not have similar cognates. Vermeij (2006) recognized the close relationship between the Pacific *Hesperisternia jugosa* (Adams, 1852), previously considered an *Engina* (Keen, 1971), *H. lauta* (Reeve, 1846), previously considered a *Cantharus* (Keen, 1971), and the Atlantic *H. karinae* (reviewed here).

A fossil record for *Engina* was nearly lacking until Landau and Vermeij (2012) reviewed the western Atlantic taxa. They identified *Engina cantaurana* Landau and Vermeij (2012) from the early Miocene of Venezuela as the oldest known member of the genus but did not believe it was closely related to any Recent species. They found that *Engina latior* Landau and Vermeij (2012) from the early Pliocene of the Dominican Republic, *E. moinensis* Landau and Vermeij (2012) from the early Pleistocene of Panamá, and *E. floridana* Olsson and Harbison, 1953, from the early Pleistocene of Florida, were more similar to Recent species. *Engina moinensis*, in particular, is very similar to the two rare, deep-water Yucatán taxa discussed here: *E. itzamnai* and *E. lignea*. The extant *E. turbinella* was recognized from the middle Miocene of Panamá (Woodring, 1973) and the late Pleistocene of the Dominican Republic (Landau and Vermeij, 2012).

Spiral and axial sculpture are features with a remarkably low degree of infraspecific variability within the genus *Engina*. Variability in pattern and color, to the contrary, is remarkably high for some *Engina*. While most species are moderately uniform in these character-

istics, without displaying much variation in pattern or color, a number of other species are strikingly variable. This was first discussed concerning a Philippine species (Fraussen and Chino, 2012); in the present paper we show a similar level of variability in at least two species.

As remarked by Cemohorsky (1975) and Faber (2007), *Engina cumingiana* Melvill, 1895, from "St. Thomas" appears to be a mislabeled, but as yet unidentified, species. It is not similar to any of the species covered here. *Engina willemsae* de Jong and Coomans (1988) was transferred to *Anna* by Watters (2009) and to *Ameranna* by Landau and Vermeij (2012). *Engina slootsi* de Jong and Coomans (1988) is *Habromorula biconica* (Blainville, 1832) (Muricidae) from the Pacific Ocean (*vide* Houart, 1994).

MATERIALS AND METHODS

Length is measured from the tip of the apex to the end of the siphonal canal. Width is measured as the maximum dimension in a plane with facing the aperture. Spiral sculpture is counted from the suture to the end of the siphonal canal. Descriptions of apertural features are based on the terminology adopted by Landau and Vermeij (2012). Lirae counts within the outer lip may include bifurcating lirations. The number of whorls was determined using the 1 D method of Van Osselaer (1999). Locality information, aside from type locality designations, may be amplified from the original label for clarification. Given the generalized nature of most label information, no attempt has been made to georeference sites that did not originally include coordinates. Dimensions in captions refer to shell length. Numbers in () following catalog numbers indicate the number of specimens in the lot.

Abbreviations used in the text are: AMNH: American Museum of Natural History, New York City, New York, USA; BSM: Bailey-Matthews National Shell Museum, Sanibel, Florida, USA; NHMUK: Natural History Museum, London, UK; EFG: Collection of Emilio F. García, Lafayette, Louisiana, USA; GTW: Collection of G. Thomas Watters, Columbus, Ohio, USA; HGL: Collection of Harry G. Lee, Jacksonville, Florida, USA; KF: Collection of Koen Fraussen, Aarschot, Belgium; MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MW: Collection of Margaret Williams, Tallevast, Florida, USA; OSUM: Ohio State University Museum of Biological Diversity, Columbus, Ohio, USA; PRI: Paleontology Research Institute, Ithaca, New York, USA; UF: Florida Museum of Natural History, Gainesville, Florida, USA; ZMA: Zoologisch Museum, Amsterdam, The Netherlands.

SYSTEMATICS

Family Buccinidae Rafinesque, 1815
Subfamily Pisaniinae Gray, 1857

Genus *Engina* Gray, 1839

Engina Gray, 1839: 112–113.

Type Species: *Engina zonata* Gray, 1839, by subsequent designation of Gray (1847) [= *Purpura turbinella* Kiener, 1835, see Orr (1962)].

Discussion: The morphological limits and unique features of *Engina* have not been easy to define. Cernohorsky (1975: 176) characterized the genus by “the radially oriented lirae [which] are found only in species of *Engina*,” a feature that Landau and Vermeij (2012) nevertheless noted was not present in all *Engina*. Landau and Vermeij (2012: 121) defined the genus by “a shell with a narrow, strongly denticulate aperture and the presence of distinct columellar folds” but admitted that “not all species... conform to this characterization.” Definitive differences between *Engina* and *Hesperisternia* appear to be particularly ambiguous. Vermeij (2009) noted that some *Hesperisternia* had shell sculpture and apertural features that were convergent with *Engina*. Watters (2009) placed *E. janowskyi* and his species *itzamnei* in *Hesperisternia*; Landau and Vermeij (2012) reallocated them to *Engina*. That reallocation is followed here and we confirm the importance of the presence of internal lirae that extend far into the aperture as an important feature to distinguish *Hesperisternia* from *Engina*.

Adding to the problems of identifying the western Atlantic species is the great variability seen in conchological features. Coloration, sculpture, degree of elongation, and apertural features are highly plastic. Given a small number of specimens it is easy to conclude that numerous taxa are involved. However, when larger lots are studied it is apparent that there are intergrades that unite such disparate forms.

The species recognized in this review are presented in alphabetical order, including the type species of *Engina*, *E. turbinella* (Kiener, 1835).

***Engina annae* new species (Figures 1–4, 13)**

Engina species.—Lee, 2009: 108, fig. 518a.

Description (based on 2 adult specimens): Larger adult specimen seen, 15.6 mm in length (holotype); smaller specimen seen, 12.9 mm in length; holotype 15.6 mm length × 8.9 mm width. Shell biconic; spire ca. 50% total length. Protoconch minute, of 1.5 smooth, pale tan whorls. Teleoconch of 5.5 whorls, demarcated from protoconch. Teleoconch sculpture of 9–10 primary rounded spiral cords, between the suture and the anterior limit of the siphonal canal, three grouped at periphery; concave or flat, wide subsutural slope with a single thin primary cord. Secondary microscopic spiral threads between primary spiral sculpture. Primary axial sculpture of broad, low, rounded ribs, very weak on subsutural slope; 10 ribs on penultimate whorl, 10 on final whorl. Extremely fine secondary wrinkles occur between axial ribs. Terminal varix weak. Aperture oval, elongate. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 5–7 denticles, decreasing in size from posterior to ante-

rior, the posterior-most two with a tendency to be weakly fused. The thin rib that projects deep into the aperture and delimits the siphonal canal found in other species is weak. Five radial lirae present at posterior end, barely distinct from columellar folds. Anterior to these are 6–8 columellar folds irregular, some lirate, others pustulose. One or more denticles extending deep into aperture, forming an interior ledge to columella. Parietal lip erect for most of its length. Siphonal canal short, open. Color gray with a tan subsutural band; axial ribs dark brown, often with a white adapertural face forming a series of dark and light spots; there is a continuous, white spiral band just below the periphery. Aperture tan with white teeth. Operculum, radula, and anatomy unknown.

Holotype: UF 479323 (ex Mark Johnson coll. 0142).

Type Locality: 33 m., 48 km off Masonboro Inlet, Wrightsville Beach, New Hanover Co., North Carolina, USA.

Paratype(s): Charlotte Thorpe coll. (1), Amberjack Hole, E of Mayport, Duval Co., Florida, USA.

Distribution: Only known from offshore of southernmost North Carolina and northeast-most Florida. We assume it occurs off the intervening South Carolina and Georgia coasts as well.

Habitat: The holotype was a crabbed specimen from 33 m, collected on sandy rubble near rocky outcrops with sponges.

Shell Variation: The known specimens are remarkably uniform in sculpture and coloration.

Etymology: Named for Ann Johnson, mother of the collector of the holotype, Mark Johnson.

Comparison with Other Species: The peculiar coloration of dark brown and white spots on a gray background has not been found in any other western Atlantic species. See Table 1 for a comparison with other species.

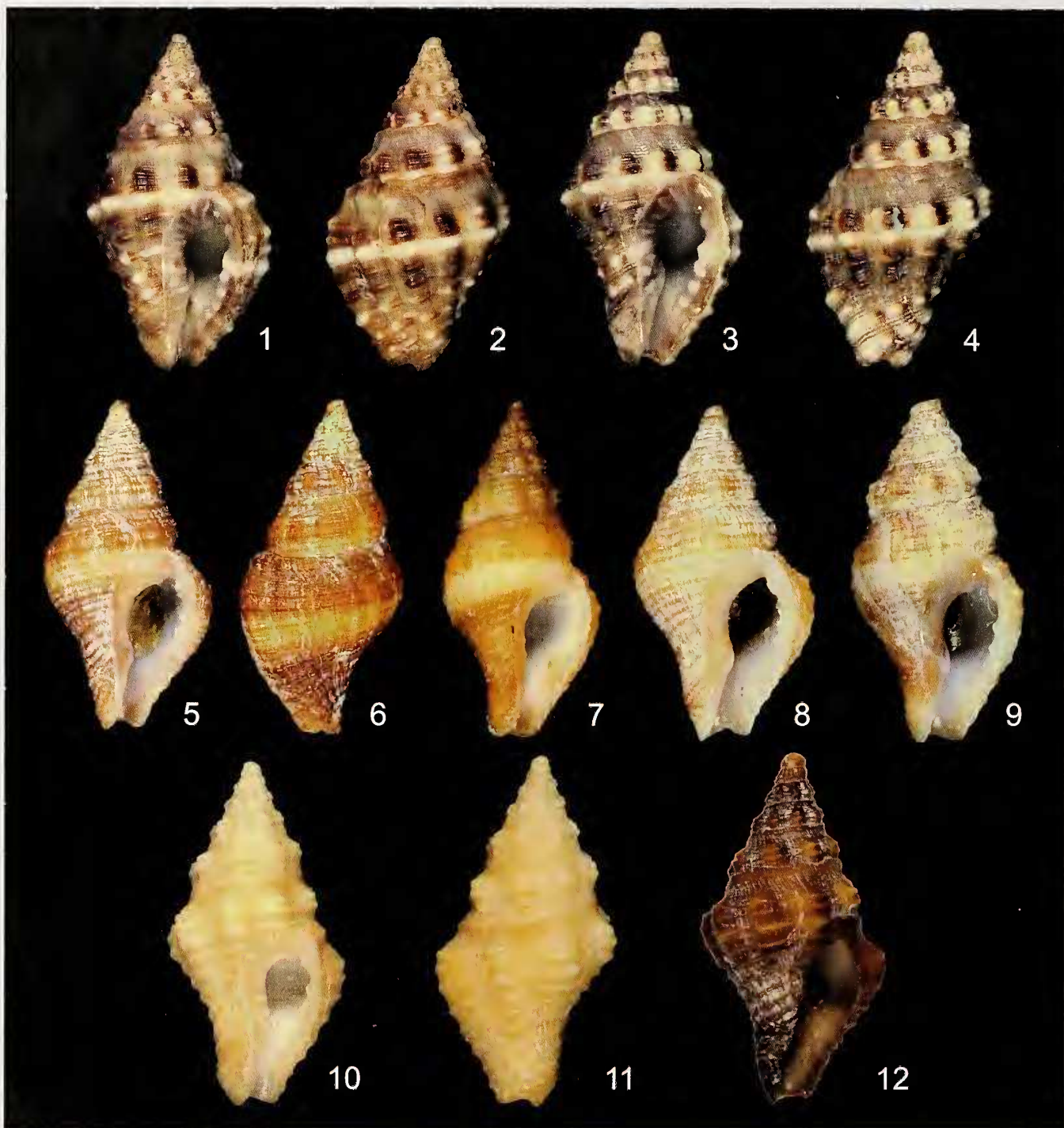
Discussion: This extremely rare species is the northernmost member of *Engina* in the western Atlantic Ocean. Like most of the species discussed here, it is an offshore species seldom encountered. It was first recognized as distinct by Lee (2009).

***Engina corinnae* Crovo, 1974 (Figures 14–33, 34)**

Engina corinnae Crovo, 1974: 30, figs. 1–3; Abbott, 1974: 217, fig. 2398; Odé, 1983: 60; Kaicher, 1986: card 4405; Landau and Vermeij, 2012: 122, 123, 126; Petuch, 2013: 202.

Engina corinnae of authors, *non* Crovo, 1971. — Lee, 2009: 108, fig. 518.

Description (based on 38 adult specimens): Largest adult specimen, 14.8 mm in length; smallest specimen, 9.2 mm in length. Shell biconic; spire ca. 50% total



Figures 1–12. *Engina* species. **1–4.** *Engina annae* new species. **1–2.** Holotype, UF 47923, 15.7 mm. **3–4.** Paratype Charlotte Thorpe coll., Amberjack Hole, E of Mayport, Duval Co., Florida, 12.9 mm. **5–9.** *Engina goncalvesi* Coltro, 2005. **5–6.** GTW 12447a, 40–50 m, in cave, off Arraial do Cabo, Rio de Janeiro State, Brazil, 11.3 mm. **7.** GTW 12447b, 150–160 m, off Cabo Frio, Rio de Janeiro State, Brazil, 13.9 mm. **8.** HGL, 40–44 m, in cave, off Arraial do Cabo, Rio de Janeiro State, Brazil, 9.5 mm. **9.** GTW 12479a, 40–50 m, in cave, off Arraial do Cabo, Rio de Janeiro State, Brazil, 11.3 mm. **10–12.** *Engina lignea* new species. **10–11.** Holotype, UF 479325, 14.3 mm. **12.** Paratype, BMSM 76001, 50–55 m, 146 km WSW of Arrecife Alacrán, Campeche Bank, Campeche State, Mexico, 11.5 mm.

length. Protoconch minute, of 1.5 smooth whorls, white with tan patches or bands. Teleoconch of 4.75–5.25 whorls, demarcated from protoconch. Teleoconch sculpture of 9–12 (mode=11) primary sharp spiral cords

between the suture and the anterior limit of the siphonal canal, weakest on concave or flat subsutural slope; elsewhere of uniform strength except that spiral cords on siphonal canal are slightly stronger. Secondary microscopic



Figure 13. Distribution of *Engina annae* new species (○), *Engina goncalvesi* Coltro, 2005 (●), *Engina lignea* new species (◆), and *Engina williamsae* new species (★).

spiral threads between primary spiral sculpture. Primary axial sculpture of broad, low ribs, absent from subsutural slope; 7–10 (mode=9) ribs on penultimate whorl, 6–13 (mode=10) on last whorl, most pronounced at periphery. Coarse secondary wrinkles occur between axial ribs which may be lamellate. Terminal varix weak. Aperture oval, elongate. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 6–8 (mode=6) denticles. The thin rib that projects deep into the aperture and delimits the siphonal canal found in other species is weak but always present. 2–5 (mode=3) radial lirae present at posterior end, weak and irregular, not distinct from columellar folds. Anterior to these are 4–7 (mode=6) semi-lirate columellar folds irregular, often limited to edge of parietal wall, weakest or absent on middle of columella. First or second anterior denticle often extending deep into aperture forming

an interior ledge to columella. Parietal lip erect for most of its length. Siphonal canal short, open. Color white or pale tan with brown blotches, darkest between axial ribs, particularly on the spire, with a wide, white sub-peripheral band; usually two fine, dark threads posterior to this band on the final whorl. Aperture white, faint tan, or mauve, darkest at anterior end. Operculum rounded, leaf-shaped, yellow with brown central radius. Radula and anatomy unknown.

Holotype: MCZ 277496.

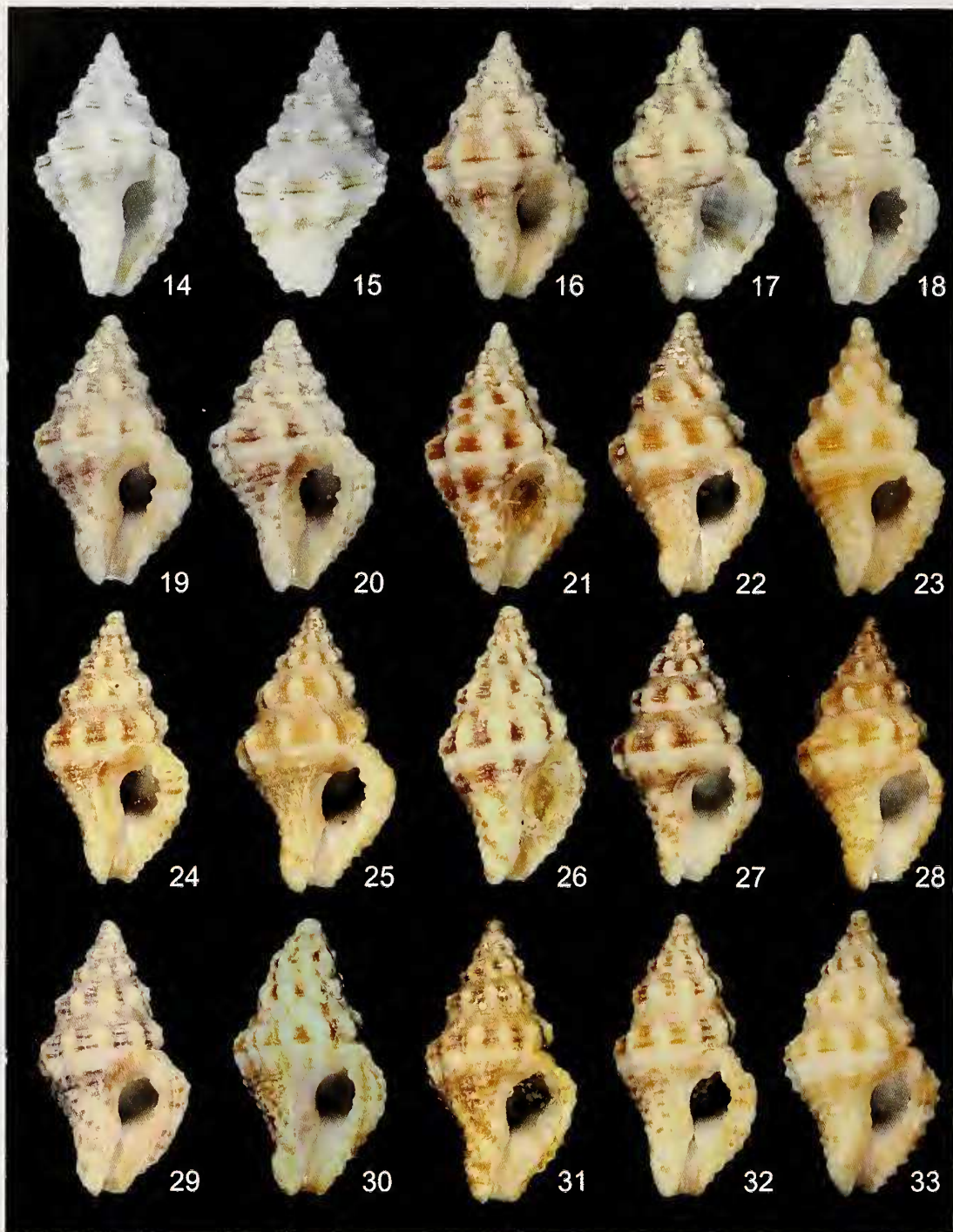
Type Locality: Off Boynton Beach, Palm Beach County, Florida, USA, 30° 00' N, –79° 57'30" W. Depth unknown.

Paratype(s): MCZ 277497 (unstated number of specimens); PRI 28273 (1); all from the type locality.

Other Material Examined (124 specimens): East Florida: MW (1), 27 m, off eastern Florida; MW (1), 34 m, off Mayport, Duval Co.; MW (1), HGL (6), 30–46 m, off St. Augustine, St. Johns Co.; UF 35241 (1), 18 m, off Boynton Beach, Palm Beach Co.; UF 128074 (66), 27 m, off Boynton Beach, Palm Beach Co.; UF 128051 (3), 27–38 m, off Boynton Beach, Palm Beach Co.; EFG 9553 (2), 38–43 m, off Boynton Beach, Palm Beach Co.; HGL (1), Boynton Beach, Palm Beach Co.; UF 352841 (1), 18 m, off Boynton Beach, Palm Beach Co., Florida; UF 122778 (7), 107 m, off Boynton Inlet, Palm Beach Co.; UF 126244 (1), 26 m, off Boynton Inlet, Palm Beach Co.; UF 228793 (6), 73 m, off Palm Beach, Palm Beach Co.; UF 127142 (1), off Palm Beach, Palm Beach Co.; UF 229058 (1), 55–73 m, off Palm Beach, Palm Beach Co.; UF 262537 (2), 91–152 m, off Palm Beach, Palm Beach Co.; UF 126241 (7), 37 m, off Palm Beach, Palm Beach Co.; UF 228990 (2), 37–46 m, off Palm Beach Inlet, Palm Beach Co.; UF 250037 (2), 37–55 m, Dodge Estate to inlet, Palm Beach Co.; EFG 13895 (1), 30 m, off West Palm Beach, Palm Beach Co.; HGL (3), 183–213 m, off Looe Key, Monroe Co. West Florida: EFG 28347 (1), 61 m, off Egnont Key, Hillsborough Co.; MW (1), HGL (5), 27 m, off Panama City, Bay Co.; MW (2), 6.4 km off

Table 1. Shell characteristics of *Engina* and *Hesperisternia*. Numbers in () are modes except for length, which are averages; * – no mode.

Taxon	Number of Radial Lirae	Number of Columellar folds	Number of Outer Lip Denticles	Anterior Outer lip Lira	Number of Axial Ribs Last Whorl	Number of Axial Ribs Pen. Whorl	Primary Spiral Cords Last Whorl	Length
<i>annae</i>	5	6–8	5–7	weak	10	10	9–10	12.9–15.6
<i>corinnae</i>	2–5 (5)	4–7 (6)	6–8 (6)	weak	6–13 (10)	7–10 (9)	9–12 (11)	9.2–14.8 (12.4)
<i>demani</i>	2–4 (3)	4–8 (6)	5–6 (5)	N	6–8 (7)	6–8 (7)	10–12 (12)	11.7–15.5 (13.8)
<i>goncalvesi</i>	1	3–5 (*)	6–7 (*)	N	obsolete	8–11 (10)	12–15 (12)	9.5–14.2 (11.5)
<i>karinae</i>	irregular	irregular	8–10 (*)	N	7–10 (9)	7–10 (9)	9–11 (9)	17.9–25.0 (20.1)
<i>lignea</i>	5	5	5	Y	7	7	9–10	14.3
<i>permixta</i>	3–5 (4)	4–7 (5)	3–6 (5)	Y	7–10 (9)	8–10 (8)	7–10 (9)	9.4–16.1 (12.5)
<i>itzamnai</i>	2	5	4	N	8–10 (*)	8–10 (*)	11–13 (*)	17.4–17.8 (17.6)
<i>turbinella</i>	3–7 (4)	4–8 (6)	3–7 (6)	Y	8–13 (10)	9–14 (10)	6–10 (8)	6.6–14.9 (9.8)
<i>williamsae</i>	2–5 (4)	2–6 (*)	5–6 (5)	weak	8–10 (9)	9–10 (9)	9–11 (9)	11.5–15.0 (13.4)



Figures 14–33. *Engina corinnae* Crovo, 1974. 14–15. Holotype, MCZ 277496, photo courtesy of Jennifer W. Lenihan, © Museum of Comparative Zoology, Harvard Univ., 13.0 mm. 16. UF 128074, 27 m, off Boynton Beach, Palm Beach Co., Florida, 12.4 mm. 17. EFG 9553, 38–43 m, off Boynton Beach, Palm Beach Co., Florida, 9.9 mm. 18. UF 228793, 73 m, off Palm Beach, Palm Beach Co., Florida, 9.5 mm. 19. UF 122778, 107 m, off Boynton Inlet, Palm Beach Co., Florida, 9.3 mm. 20. UF 122778, 107 m, off Boynton Inlet, Palm Beach Co., Florida, 9.3 mm. 21. UF 126241, 36.6 m, off Palm Beach, Palm Beach Co., Florida, 11.0 mm. 22. MW, 30–46 m, off St. Augustine, St. Johns Co., Florida, 12.7 mm. 23. HGL, 183–213 m, off Looe Key, Monroe Co., Florida, 11.5 mm. 24. HGL, 30–46 m, off St. Augustine, St. Johns Co., Florida, 12.2 mm. 25. MW, 6.4 km off Panama City, Bay Co., Florida, 13.2 mm. 26. HGL, 30–46 m, off St. Augustine, St. Johns Co., Florida, 10.5 mm. 27. EFG 13895, 30 m, off West Palm Beach, Palm Beach Co., Florida, 14.2 mm. 28. EFG 27567, 39 m, 54 km SSW of Panama City, Bay Co., Florida, 14.7 mm. 29. MW, 27 m, off Panama City, Bay Co., Florida, 10.5 mm. 30. MW, 31 m, off NE Yucatan, Mexico, 14.8 mm. 31. EFG 28347, 61 m, off Egmont Key, Hillsborough Co., Florida, 12.6 mm. 32. MW, 34 m, off Mayport, St. Johns Co., Florida, 12.7 mm. 33. ?*Engina corinnae*. UF 352841, 18 m, off Boynton Beach, Palm Beach Co., Florida, 12.4 mm.



Figure 34. Distribution of *Engina corinnae* Crovo, 1974 (○) and *Engina demani* de Jong and Coomans, 1988 (●).

Panama City, Bay Co.; EFG 27567 (1), 39 m, 54 km SSW of Panama City, Bay Co., 29° 43.32' N, -85° 54.85' W. Louisiana: EFG 23426 (1), 57–65 m, Ewing Bank, 105 km off Louisiana coast, 28° 06.07' N, -91° 02.42' W. Mexico: MW (3), 31 m, off NE Yucatán.

Lee (2009) also lists Xalvis Island, St. Johns Co., Florida.

Distribution: Western Atlantic Ocean, offshore, eastern Florida from St. Johns County to the Florida Keys. Gulf of Mexico from Hillsborough County, Florida, west to Louisiana, and off Yucatán Peninsula. The *E. corinnae* recorded from the East Flower Garden banks by Odé (1983) may be this species but we have not seen the specimen. This species co-occurs with the equally rare *E. williamsae* at Egmont Key off Tampa Bay, western Florida.

Habitat: Empty shells have been found from 18–122 m on rubble bottom. Live specimens have been recorded from 30–73 m. Specimens are locally common and are occasionally found on *Spondylus*. Most specimens are taken as by-catch by shrimp and scallop trawlers. A single label reads “rock, sand reef,” the only report of a habitat. Specimens are frequently covered by calcareous algae.

Variation in Specimens: Specimens vary in degree of coloration, from nearly all white (holotype) to having prominent brown patches. The intervarical brown banding varies from diffuse patches to distinctly pigmented spiral cords, but is always present. Specimens also vary in the degree of elongation, ranging from compact to rather fusiform.

Etymology: Named for Corinne E. Edwards (1905–1989), an “ardent collector of marine life as well as an

educator in popular subjects on natural history” (Crovo, 1974: 30).

Comparison with Other Species: *Engina corinnae* superficially resembles *E. williamsae* new species. *Engina corinnae* has more prominent spiral sculpture over the entire shell, including the sub-sutural band, which is nearly smooth in *E. williamsae*. *Engina corinnae* is also less solid, has a shorter spire, and averages a slightly smaller size. The widespread *E. turbinella* differs in its (usually) much darker coloration with white spots as contrasted to the lighter coloration with dark spots seen in *E. corinnae*, as well as its dark aperture with white teeth. See Table 1 for a comparison with other species.

Discussion: *Engina corinnae* is an offshore species that varies greatly in the degree of elongation and coloration. The holotype is not typical of the specimens usually seen. It is small, compact, nearly uniformly white, and has fewer axial ribs than average specimens.

Engina demani de Jong and Coomans, 1988 (Figures 34–49)

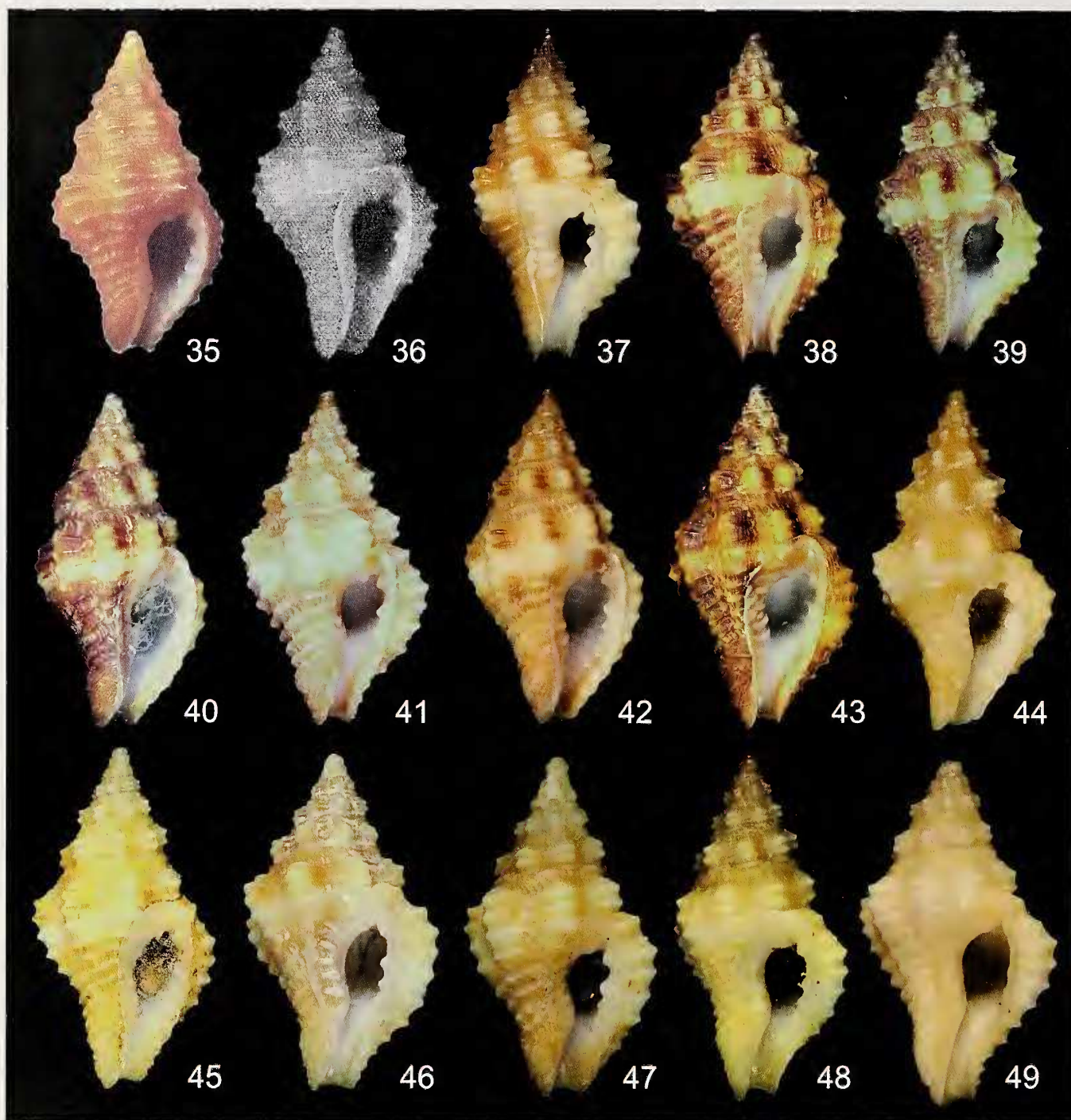
Engina demani de Jong and Coomans, 1988: 83, pl. 38, fig. 451; Faber, 2007: 74, figs. 1–3; Watters, 2009: 271.

Engina janowskyi Coltro, 2005: 1, pl. A, figs. 1–5; Faber, 2007: 74, figs. 6, 7; Dornellas and Simone, 2011: 20; Landau and Vermeij, 2012: 123, 125, 126.

Hesperisternia janowskyi (Coltro, 2005). — Watters, 2009: 271.

Engina demanorum [sic] de Jong and Coomans, 1988. — Landau and Vermeij, 2012: 123, 125, 126 [unjustified emendation, see “etymology” below].

Description (based on 20 adult specimens): Largest adult specimen, 15.5 mm in length; smallest specimen, 10.7 mm in length. Shell biconic to fusiform; spire ca. 50% total length. Protoconch small, conical, of 1.5–1.75 smooth, white or brown banded whorls. Teleoconch of 5.5 whorls, weakly demarcated from protoconch. Teleoconch sculpture of 10–12 (mode=12) evenly spaced, rounded, spiral cords between the suture and the anterior limit of the siphonal canal. Subsutural slope wide, flat, with single primary thread, well-developed in some specimens, very weak in others. Between these cords are ca. 10 fine, regular threads. Axial sculpture of widely spaced, wide, primary angular ribs; 7 (rarely 6 or 8) on the final whorl, 7 (rarely 6 or 8) on penultimate whorl, most prominent on periphery, with numerous secondary fine, axial threads in between primary ribs; in well-preserved specimens these threads are developed into oblique lamella, giving a scalloped appearance to the sculpture. Terminal varix well-developed, angular. Aperture oval. Parietal wall erect on anterior half. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 5 (rarely 6) small denticles. The thin rib that projects deep



Figures 35–49. *Engina demani* de Jong and Coomans, 1988. **35.** Holotype, *Engina demani* de Jong and Coomans, 1988, 11.0 mm, photo courtesy of Marien Faber. **36.** Holotype, *Engina janowskyi* Coltro, 2005, 13.2 mm, reproduced from Coltro (2005). **37.** HGL, 183 m, 3.2 km W of Sandy Lane Bay, Barbados, 11.2 mm. **38.** GTW 13795e, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 13.8 mm. **39.** GTW 13795e, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 15.2 mm. **40.** HGL, 40–45 m, off Búzios, São Paulo State, Brazil, 10.7 mm. **41.** HGL, shallow water, Cartagena, Colombia, 13.6 mm. **42.** GTW 13795a, 40–45 m, Ilha de Cabo Frio, Rio de Janeiro State, Brazil, 13.5 mm. **43.** GTW 12026d, 3 m, off Guarapari, Espírito Santo State, Brazil, 15.0 mm. **44.** GTW 15579a, French Guiana, 13.1 mm. **45.** GTW 13795b, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 15.3 mm. **46.** GTW 11645a, 15–25 m, off Guarapari, Espírito Santo State, Brazil, 12.3 mm. **47.** GTW 13795e, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 12.3 mm. **48.** GTW 13795b, 4 m, Ilha Escalvada, Espírito Santo State, Brazil, 11.4 mm. **49.** GTW 13795e, off Guarapari, Espírito Santo State, Brazil, 14.9 mm.

into the aperture and delimits the siphonal canal found in other species is absent or nearly so. Radial lirae 1–4 (mode=3) (may be bi- or trifurcate) at posterior end, weak and irregular, not very distinct from columellar folds. Anterior to these are columellar folds (4–8, mode=6) weak, irregular, often limited to edge of parietal wall. Swelling on interior ledge of columella not pronounced. Siphonal canal moderately short, open. Base color variable: dark brown, tan, or yellow, axial ribs usually darker, always with a continuous pale band just anterior to the periphery. The abapertural side of the axial ribs is usually dark-colored and the adaperture side is usually pale. Aperture white to tan, the siphonal canal rimmed in brown. Operculum oval, yellow-brown, with a subterminal nucleus. Radula and anatomy unknown.

Holotype: *Engina demani* de Jong and Coomans, 1988: ZMA 3.87.084; *Engina janowskyi* Coltro, 2005: Museu de Zoologia da Universidade de São Paulo 37178, but apparently lost (*fide* D. Cavallari, Jan. 2015).

Type Locality: *Engina demani* de Jong and Coomans, 1988, Aruba, harbour [Netherlands Antilles]. *Engina janowskyi* Coltro, 2005, off Guarapari, Espírito Santo State, Brazil.

Paratype(s): *Engina demani* de Jong and Coomans, 1988: Faber (2007) illustrated a “paratype” from the Frère Fredericus Verberne collection. Although de Jong and Coomans (1988) mentioned additional examples in the Verberne and de Man collections, they are not explicitly referred to as types and it is not certain whether these specimens are valid paratypes. *Engina janowskyi* Coltro, 2005: Museu Oceanográfico Eliézer Rios da Funfação Universidade de Rio Grande 43853; Museu Nacional da Universidade Federal do Rio de Janeiro, unnumbered; P.M. Santos Costa coll.; R. Janowsky coll. [all single specimens]. The localities of the paratypes were not given but are presumed to be from the type locality.

Other Material Examined (28 specimens): Barbados: HGL (1), 183 m, 3.2 km W of Sandy Lane Bay. Colombia: HGL (1), shallow water, Cartagena. French Guiana: GTW 15579a (1). Brazil: GTW 11645a (3), HGL (1), 15–25 m, off Guarapari, Espírito Santo State; GTW 13795c (1), 25 m, off Guarapari, Espírito Santo State; GTW 12026c (2), 12026d (4), 3 m, off Guarapari, Espírito Santo State; HGL (1), 18 m, off Anchieta, Espírito Santo State; GTW 13795b (3), 13795e (5), 4 m, Ilha Escalvada, Espírito Santo State; GTW 13795a (1), 40–45 m, Ilha de Cabo Frio, Rio de Janeiro State; HGL (1), 34–45 m, off Búzios, São Paulo State; HGL (3), 40–45 m, off Búzios, São Paulo State.

Distribution: Apparently widely distributed across the southern Caribbean and down the Brazilian coast to São Paulo State, but this is based on few records with large gaps.

Habitat: Empty shells are found at depths between 3–183 m; some live specimens have been collected in caves at 40–45 m, but the majority of specimens examined were found on rubble or under rocks from 4 m.

Variation in Specimens: Shell base color varies from nearly pure white to nearly all dark brown. Elongation varies from compact, solid shells (typically from Brazil, Figures 38, 43) to relatively high-spined, narrow shells (French Guiana, Figure 44). Despite this great variation in color and elongation of the shell, the sculpture is remarkably uniform in the number of axial and spiral elements.

Etymology: *Engina demani* de Jong and Coomans, 1988, named for Ad and Gon de Man, shell collectors in Aruba. Thus the correct orthography should be *demanorum*. However, a name change reflecting this would be an unjustified emendation. *Engina janowskyi* Coltro, 2005, named for Robert H. Janowsky, owner of MdM Shell Books in Wellington, Florida, USA.

Comparison with Other Species: Some color forms of *E. permixta* are similar to *E. demani*, with which it may be sympatric. *Engina permixta* has more axial ribs on both the final whorl (7–10) and the penultimate whorl (8–10) than does *E. demani* (6–8 for both) and has fewer spiral cords on the final whorl (7–10 vs. 10–12). Additionally, the deep ridge bounding the siphonal canal on the inside of the outer lip is present in *E. permixta* but absent or very weak in *E. demani*. See Table 1 for a comparison with other species.

Discussion: This is a very variable species in coloration, in degree of elongation, and in the strength of the sculpture. *Engina demani* is based on short, compact specimens. *Engina janowskyi* is based on elongate forms. Without seeing intermediates, the two forms would clearly seem to represent two taxa. However, there is no clear cut delineation between the two forms in either color or elongation and the two taxa are synonymous. This possible synonymy was first suggested by Faber (2007), who remarked that *E. demani* may be the shallow water form and *E. janowskyi* the deeper water form. However, our records indicate that there is great variation within each population regardless of depth and both “forms” and intergrades co-occur together.

Engina gonalvesi Coltro, 2005 (Figures 5–9, 13)

Engina gonalvesi Coltro, 2005: 1–2, pl. B, figs. 1–11; Faber, 2007: 74 [in synonymy of *Bailya milleri* Nowell-Usticke, 1959]; Watters, 2009: 270–271, figs. 190, 191; Dornellas and Simone, 2011: 17; Landau and Vermeij, 2012: 123.

Description (based on 4 adult specimens): Largest adult specimen, 14.2 mm in length; smallest specimen, 9.5 mm in length. Shell fusiform; spire ca. 50% total length. Protoconch small, of 1.5 smooth, brown whorls

with pale peripheral band. Teleoconch of 5 whorls, abruptly arising from protoconch. Teleoconch sculpture of 12–15 (mode=12) primary flattened, spiral threads on final whorl between the suture and the anterior limit of the siphonal canal, with numerous intercalated secondary and tertiary threads. Spiral cords on siphonal canal slightly stronger. Axial sculpture of broad, low ribs; ca. 20 primary ribs on penultimate whorl, obsolete on most specimens by last whorl. Intersections of axial and spiral sculpture with weak, elongated nodules. Terminal varix well-developed, flaring, moderately narrow. Aperture oval. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 6–7 weak, irregular denticles. The thin rib that projects deep into the aperture and delimits the siphonal canal found in other species is absent. Single (or bifurcating) radial lira at posterior end, very weak and irregular, not very distinct from columellar folds. Anterior to this lira are columellar folds (3–5), usually indistinct, irregular, often limited to edge of parietal wall. Swelling on interior ledge of columella distinct, white. Parietal lip erect for most of its length. Siphonal canal short, open. Color brown with wide, pale tan spiral band at subperiphery, primary spiral cords often darker. Aperture with brownish-purple tinge. Operculum leaf-shaped, golden-tan, with anterior terminal nucleus. Radula and anatomy unknown.

Holotype: Stated to be in Museu de Zoologia da Universidade de São Paulo, 37179, and listed as such in Dornellas and Simone (2011), but not found (*vide* L. R. L. Simone, pers. comm., 2008).

Type Locality: Off Cabo Frio, Rio de Janeiro State, Brazil. Depth unknown.

Paratype(s): Museu Oceanográfico Eliézer Rios da Fundação Universidade de Rio Grande 43854 (1); Museu Nacional da Universidade Federal do Rio de Janeiro, unnumbered (2); P.M. Santos Costa coll. (1). The localities of the paratypes were not given but are presumed to be from the type locality.

Other Material Examined (4 specimens): **Brazil.** GTW 10479a (1), 12477a (1), 40–50 m, in cave, off Arraial do Cabo, Rio de Janeiro State; HGL (1), 40–44 m, in cave, off Arraial do Cabo, Rio de Janeiro State; GTW 12477b (1), 150–160 m, off Cabo Frio, Rio de Janeiro State.

Distribution: Brazil, between Cabo Frio, Rio de Janeiro State, and Ilhabela, São Paulo State.

Habitat: Empty shells are found between depths of 25–160 m; live individuals from 25–45 m under rocks, sometimes in caves.

Variation in Specimens: The few specimens we have seen are very uniform in all characteristics.

Etymology: Named for Paulo Cesar Pinto Gonçalves, who first collected the species.

Comparison with Other Species: The near lack of axial sculpture on the final whorl and reduced columellar dentition set this species apart from all other western Atlantic *Engina*. See Table 1 for a comparison with other species.

Discussion: This species is placed in *Engina* with some reservation. The parietal shield lirae and columellar folds are nearly absent in some specimens and only barely expressed in the remainder.

***Engina itzamnai* (Watters, 2009)
(Figures 50–57, 68)**

Hesperisternia itzamnai Watters, 2009: 271, figs. 192–195, 264.

Engina itzamnai (Watters, 2009). — Landau and Vermeij, 2012: 123.

Engina dicksoni Petuch, 2013: 72, 192, 202, fig. 5.6E.

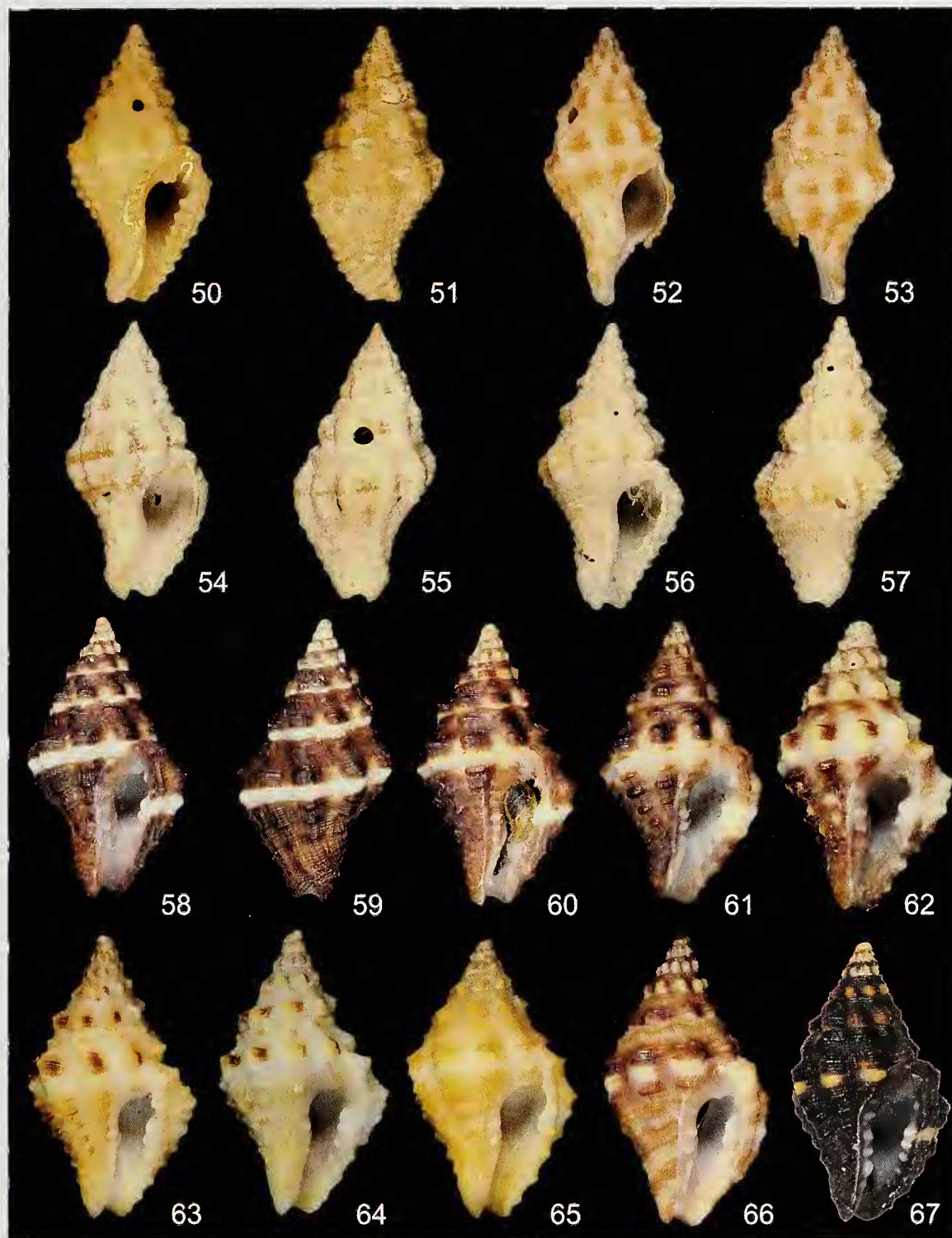
Description (based on 4 specimens): Largest adult specimen, 17.8 mm in length (holotype); smallest adult specimen, 17.4 mm in length. Shell fusiform; spire ca. 50% total length. Shell relatively thin. Protoconch small, conical, of 1.5 smooth, white whorls with tan blotches. Teleoconch of 5.5 whorls, strongly demarcated from protoconch. Teleoconch sculpture of 11–13 rounded, widely separated primary spiral cords between the suture and the anterior limit of the siphonal canal, with numerous intercalated secondary threads. Subsutural slope wide, flat, with single primary thread. Spiral cords on siphonal canal slightly stronger. Axial sculpture of widely spaced, rounded primary ribs; 8–10 on penultimate whorl, 8–10 on final whorl, with numerous secondary axial threads. Intersections of axial and spiral sculpture with strong, elongated nodules, strongest at periphery. Terminal varix weakly developed, somewhat constricted, narrow. Aperture oval, outer lip with 4 medial teeth. Anal canal deeply indented between two teeth; columellar tooth bifid. Parietal wall erect with 7 weak, lirate teeth. Siphonal canal moderately long, open. Color white with orangish-tan interaxial spaces cut by a white subperipheral narrow band; the spaces form broken flammulations below this band. Aperture white. Operculum, radula, and anatomy unknown.

Holotype: *Hesperisternia itzamnai* Watters, 2009, UF 170226. *Engina dicksoni* Petuch, 2013, UF 328420.

Type Locality: *Hesperisternia itzamnai* Watters, 2009: 100 fms. [91 m], NE of Contoy Light, Isla Contoy, Quintana Roo State, México: *Engina dicksoni* Petuch, 2013: 35 m depth on Campeche Bank, off Puerto Progreso, Yucatán State, Mexico.

Paratype(s): *Hesperisternia itzamnai* Watters, 2009, UF 425817 (1), from type locality. *Engina dicksoni* Petuch, 2013, Petuch coll. (1), from type locality.

Other Material Examined (2 specimens): Mexico: EFG 25800 (1), 52–53 m, 64 km NNW of Cayos



Figures 50–67. *Engina* species. **50–57.** *Engina itzamnai* (Watters, 2009). **50–51.** Holotype, UF 170226, 17.9 mm. **52–53.** Paratype, UF 425817, 91 m, NE of Contoy Light, Isla Contoy, Quintana Roo State, Mexico, 16.2 mm. **54–55.** MW, 31 m, off NE Yucatan, Campeche State, Mexico, 17.4 mm. **56–57.** EFG 25800, 52–53 m, 64 km NNW of Cayos Arcas, Campeche Bank, Campeche State, Mexico, 17.4 mm. **58–67.** *Engina permixta* new species. **58–59.** Holotype, UF 479326, 16.1 mm. **60.** Paratype, UF 479324, from type locality, 14.5 mm. **61.** Paratype, OSUM 39958, 21 m, off Piúma, Espírito Santo State, Brazil, 12.7 mm. **62.** GTW 4265f, 20–25 m, off Guarapari, Espírito Santo State, Brazil, 11.4 mm. **63.** GTW 4265b, 21 m, off Piúma, Espírito Santo State, Brazil, 13.0 mm. **64.** GTW 13807a, 40–50 m, off Conceição da Barra, Espírito Santo State, Brazil, 12.0 mm. **65.** GTW 4265r, from type locality, 12.1 mm. **66.** GTW 12026a, 40–45 m, off Búzios, Rio de Janeiro State, Brazil, 11.2 mm. **67.** GTW 4265ah, 10–15 m, Porto da Barra, Salvador, Bahia State, Brazil, 12.4 mm.



Figure 68. Distribution of *Engina itzamnai* (Watters, 2009) (○) and *Hesperisternia karinae* (Nowell-Usticke, 1959) (●).

Arcas, Campeche Bank, Campeche State, 20° 45.59' N, -92° 12.63' W; MW (1), 31 m, off NE Yucatán, Campeche State.

Distribution: Gulf of Mexico, Campeche Bank between Arrecife Alacrán and Cayos Arcas.

Habitat: Dead specimens were dredged in 46–180 m on rubble bottom. No live collected specimens are known to us.

Variation in Specimens: The few known specimens vary slightly in the number of axial (8–10) and spiral (11–13) sculptural elements.

Etymology: *Hesperisternia itzamnai* Watters, 2009: Mayan, *Itzamná*, the creator deity in Mayan mythology. This species is only known from off the Yucatán Peninsula, ancestral home of the Mayans. A masculine name. *Engina dicksoni* Petuch, 2013: Named for Andrew Dickson, collector of the type.

Comparison with Other Species: This is the largest western Atlantic *Engina* and the most fusiform. See comparison with *E. lignea* new species, below. See Table 1 for a comparison with other species.

Discussion: This is apparently a very rare species in collections. Petuch (2013) renamed this taxon *Engina dicksoni*.

Engina lignea new species (Figures 10–13)

Description (based on 2 specimens): Only adult specimen seen, holotype 14.3 mm in length × 7.4 mm in width. Fusiform; spire ca. 50% total length. Shell thick,

solid. Protoconch small, conical, of 1.5 smooth, tan whorls. Teleoconch of 5 whorls, strongly demarcated from protoconch. Teleoconch sculpture of 9–10 rounded, widely separated primary spiral cords between the suture and the anterior limit of the siphonal canal, with 3–6 intercalated secondary threads. Subsutural slope wide, flat, with single primary thread. Axial sculpture of widely spaced, rounded primary ribs; 7 on penultimate whorl, 7 on final whorl, with numerous secondary very fine, axial threads. Intersections of axial and spiral sculpture with strong, elongated nodules, strongest at periphery. Terminal varix weakly developed, low and wide. Aperture oval, outer lip with 5 lirate denticles extending deep into aperture. Anal canal shallowly indented between two weak teeth. Parietal wall erect anteriorly with 5 lirate columellar folds. Siphonal canal moderately long, open. Color uniformly light tan to brown, with a vague darker band on sub-sutural plane, with or without lighter-colored peripheral axial nodes. Aperture light tan. Operculum, radula, and anatomy unknown.

Holotype: UF 479325 (ex EFG 26687).

Type Locality: 46–48 m, 145 km WSW of Arrecife Alacrán, Campeche Bank, Campeche State, México, 22° 10.80' N, -91° 09.00' W.

Paratype(s): BMSM 76001(1), 50–55 m, 146 km WSW of Arrecife Alacrán, Campeche Bank, Campeche State, México, 22° 11.46' N, -91° 08.71' W (ex EFG 25822).

Distribution: Known only from off northern Yucatán Peninsula.

Habitat: Only empty shells have been found between 46–55 m.

Variation in Specimens: The two known specimens differ in color from light tan to dark brown.

Etymology: Latin *lignea*, made of wood, in reference to the texture and colors of the shells.

Comparison with Other Species: This species is most similar to the sympatric *E. itzamnai*. It is a smaller species that differs in having fewer primary axial ribs on both the final whorl (8–10 in *E. itzamnai*, 7 in *E. lignea*) and on the penultimate whorl (8–10 in *E. itzamnai*, 7 in *E. lignea*), as well as fewer primary spiral cords (11–13 in *E. itzamnai*, 9–10 in *E. lignea*). See Table 1 for a comparison with other species.

Discussion: This is the second new *Engina* described from the Yucatán Peninsula. Both are deeper water species that are rare in collections. Both have some characteristics of *Hesperisternia* but based on the analysis of Landau and Vermeij (2012) we have placed them in *Engina*.

Engina permixta new species (Figures 58–67, 103)

non Engina turbinella (Kiener, 1836). — Rios, 1975: 93, pl. 27, fig. 385; Coltro, 2005: 1, pl. A, figs. 8–10 [misidentifications].

?*Engina turbinella* (Kiener, 1836). — Lopes and Alvarenga, 1955: 173; Kempf and Matthews, 1968: 93; Matthews and Kempf, 1970: 32, 46; Eston et al., 1986: 43; Leal, 1991: 153.

Description (based on 31 adult specimens): Largest adult specimen, 16.1 mm in length (holotype); smallest specimen, 9.4 mm in length; holotype 16.1 in length \times 8.3 mm in width. Shell biconic; spire ca. 50% total length. Protoconch small, conical, of 1.5 smooth, white or brown banded whorls; last $\frac{1}{4}$ whorl may have axial folds. Teleoconch of 5.5 whorls, strongly demarcated from protoconch. Teleoconch sculpture of 7–10 (mode=9) primary spiral cords between the suture and the anterior limit of the siphonal canal. Subsutural slope wide, flat, with single primary cord. Three primary cords gathered at periphery, remaining cords very widely spaced, flattened or nodulose. 5–6 uniformly wide secondary threads between these remaining cords. Axial sculpture of widely spaced, angular primary ribs; 7–10 (mode=9, but often 8) on the final whorl, 8–10 (mode=8) on penultimate whorl, axial sculpture most prominent on periphery, with numerous secondary fine, axial threads in between primary ribs. Terminal varix only slightly more prominent than preceding axial ribs, angular. Aperture oval. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 3–6 (mode=5) weak, irregular denticles, posterior-most 2 often fused. The thin rib that projects deep into the aperture and delimits the siphonal canal found in other species is weak but always present. 3–5 (mode=4) radial lira present at posterior end, weak and irregular, not very distinct from columellar folds. Anterior to these are 3–7 (mode=5) denticulate columellar folds, irregular, often limited to edge of parietal wall. Second or third anterior denticle often extending deep into aperture. Anterior-most denticle may form a ridge extending along the parietal wall to the anterior margin. Interior ledge of columella well-defined, often merging with anterior-most denticle. Siphonal canal moderately short, open. Base color variable: dark brown, tan, or yellow, axial ribs usually darker, always with a continuous white band just anterior to the periphery; this band may have yellow portions to it. Aperture white to tan. Operculum oval, yellow-brown, with a subterminal nucleus. Radula and anatomy unknown.

Holotype: UF 479326 (ex GTW 4265r).

Type Locality: 1 m, Cajueiro, Rio Grande do Norte State, Brazil.

Paratype(s): BMSM 76000 (1), from type locality (ex GTW 4265r); OSUM 39958 (1), 21 m, off Piúma, Espírito Santo State, Brazil (ex GTW 13807b); UF 479324 (1), from type locality (ex GTW 4265r). Other Material Exam-

ined (51 specimens): Brazil: GTW 13807c (6), 1 m, Cajueiro, Rio Grande do Norte State; MW (3), intertidal, Ilha do Frade, Fernando de Noronha, Pernambuco State; UF 126233 (2), Ponta Verde, Maceió, Alagoas State; MW (1), 1 m, Maragogi, Alagoas State; GTW 4265ah (2), EFG 14667 (3), 10–15 m, Porto da Barra, Salvador, Bahia State; MW (5), Monte Serrat, Bahia State; MW (1), Barra, Salvador, Bahia State; GTW 13807a (1), 40–50 m, off Conceição da Barra, Espírito Santo State; GTW 13807b (2), KF 7343 (1), 21 m, off Piúma, Espírito Santo State; HGL (1), 15–25 m, off Guarapari, Espírito Santo State; GTW 4265f (1), GTW 4265o (1), GTW 4265s (2), HGL (2), 20–25 m, off Guarapari, Espírito Santo State; HGL (1), 10–25 m, off Guarapari, Espírito Santo State; GTW 13807d (2), 60–80 m, off Guarapari, Espírito Santo State; KF 6123, 45–60 m, off Guarapari, Espírito Santo State (1); KF 4928, 15–30 m, off Guarapari, Espírito Santo State (2); KF 80 (1), Rio de Janeiro, Rio de Janeiro State; GTW 12026a (6), GTW 12026b (1), HGL (1), 40–45 m, off Búzios, Rio de Janeiro State; HGL (1), 35–45 m, off Búzios, Rio de Janeiro State; HGL (1), 40–46 m, off Búzios, Rio de Janeiro State.

Distribution: Brazil, from Rio Grande do Norte State to São Paulo State; Fernando de Noronha. If the specimens referred to *E. turbinella* by Leal (1991) are this species, then it is also present at Abrolhos, Atol das Rocas, Jaseur, and Davis and Dogaressa seamounts.

Habitat: Empty shells have been found from low tide to 50 m; live individuals have been found from 1–45 m under rocks and on rubble.

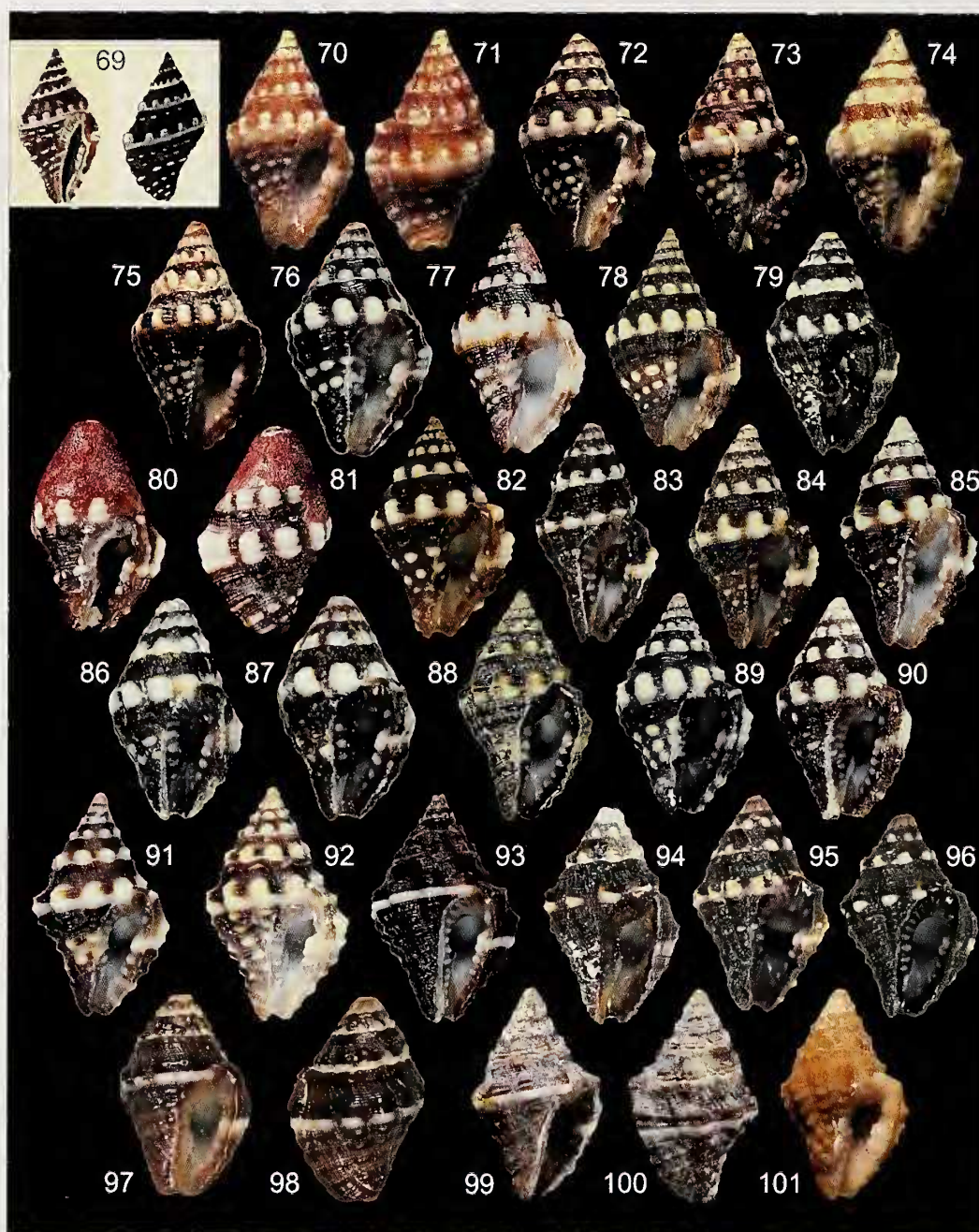
Variation in Specimens: Shell coloration varies from nearly all dark brown to nearly all pale yellow to white, with all intergrades. There is no clinal variation in shell color and all colors may occur together. The dark brown morph characterized by the holotype appears to be the most common.

Etymology: Latin *permixta*, mixed, confused, in relation to the disarray of color forms.

Comparison with Other Species: Although often misidentified as *E. corinnae*, it is not similar to that Florida-Gulf of Mexico species. It is most similar to some color forms of *E. demani*, with which it may co-occur. See the comparison under that species for details. See Table 1 for a comparison with other species.

Discussion: The somewhat weathered lectotype of *Engina zonata* Gray, 1839, is very close to some specimens of this species. However, the paralectotype clearly shows the presence of sub-peripheral white nodules, which do not occur in *E. permixta*.

***Engina turbinella* (Kiener, 1836)
(Figures 69–100, 102)**



Figures 69–101. *Engina* species. **69–100.** *Engina turbinella* (Kiener, 1836). **69.** *Purpura turbinella* Kiener, 1836: 29, pl. 9, fig. 25. **70–71.** UF 281377, Scarborough, Tobago, 12.1 mm. **72.** KF 4735, Punto San Juan, Venezuela, 12.3 mm. **73.** UF 281378, Friendship Beach, Tobago, 11.1 mm. **74.** EFG, 60 ft., Montexuma Shoals, Mustique Island, 12.7 mm. **75.** HGL, drift, Playa de Carenera, Venezuela, 9.6 mm. **76.** EFG 25590, 3 km N of Colón Island, Panamá, 8.8 mm. **77.** GTW 4265af, 1–2 m, Buraco da Rachel, Fernando de Noronha, 9.3 mm. **78.** UF 70393, Bruja Point, Canal Zone, 15.0 mm. **79.** GTW 4265e, 0.3–1.5 m, Punta Robles, Ambergris Caye, Belize, 13.2 mm. **80–81.** NHMUK 1982122, syntype of *Engina elegans* Gray, 1839, ca. 7.5 mm, photo courtesy of Phil Hurst, NHMUK. **82.** HGL, Isla de Utila, Honduras, 11.3 mm. **83.** GTW 4265ag, 2–5 m, Isla la Tortuga, Venezuela, 13.3 mm. **84.** GTW 4265b, 7.3 m, Isla Morro Pelotas, Venezuela, 14.2 mm. **85.** UF 146654, Miami, Miami-Dade Co., Florida, 14.0 mm. **86.** GTW 4265h, 0.3–1.5 m, Long Reef, Isla Roatán, Honduras, 8.6 mm. **87.** GTW 4265c, 1 m, Sandbur Reef, Ambergris Caye, Belize, 9.3 mm. **88.** EFG 19507, Isla de Providencia, Colombia, 13.9 mm. **89.** EFG 25673, Bocas del Toro, Panamá, 10.4 mm. **90.** MW, 1.0–1.5 m, Sand Key, off Key West, Monroe Co., Florida, 11.0 mm. **91.** KF 2503, 12 m, St. Vincent, S end of Baliceaux Island, Grenadines, 12.3 mm. **92.** MW, Pompano Beach, Broward Co., Florida, 13.5 mm. **93.** KF 2551, 8–9 m, Cannoun Island, Grenadines, 13.7 mm. **94.** HGL, Current, Eleuthera, 12.1 mm. **95.** GTW 4265w, 0.6–1.8 m, Coral Cove, Mt. Hartman Bay, Grenada, 10.5 mm. **96.** GTW 4265aa, 0.3–1 m, Enrique, La Parguera, Puerto Rico, 9.7 mm. **97–98.** UF 126216, paratype of *Engina turbinella cruzana* (Nowell-Usticke, 1959), 9.2 mm. **99–100.** NHMUK 1982122, lectotype of *Engina zonata* Gray, 1839, 11.5 mm. **101.** *Engina* cf. *turbinella*. KF 5262, 12 m, Savan Island, Grenadines, 12.2 mm.



Figure 102. Distribution of *Engina pernixta* new species (○) and *Engina turbinella* (Kiener, 1836) (●) (not shown, *E. turbinella* record from Fernando de Noronha).

Buccinum B.r. *parvum*, *striatum*, *asperum*, *ex albo*...
Lister, 1685: pl. 953, fig. 3.

Purpura turbinella Kiener, 1836: 29, pl. 9, fig. 25.

Engina zonata Gray, 1839: 113; Tryon, 1883: 196, 247; Bartsch, 1931: pl. 1, fig. 6; Faber, 2007: 73 [in synonymy of *Purpura turbinella* Kiener, 1836]; Fraussen and Chino, 2011: 64 [in synonymy of *Purpura turbinella* Kiener, 1836]; Landau and Vermeij, 2012: 122 [in synonymy of *Purpura turbinella* Kiener, 1836].

Engina elegans Gray, 1839: 113; Tryon, 1883: 192, 213 [in synonymy of *Purpura turbinella* Kiener, 1836]; Pace, 1902: 78.

Ricinus turbinella (Kiener, 1836). — Reeve, 1846: species 42, pl. 5, fig. 42.

Enzina [sic] *zonata* Gray, 1847: 133; Tomlin, 1928: 40.

Turbinella (*Fusus*) *elegans* (Gray, 1839). — Tryon, 1881: 97.

Engina turbinella (Kiener, 1836). — Tryon, 1883: 192, 213, 244, pl. 62, figs. 38, 39; Dall and Simpson, 1901: 402; Warmke and Abbott, 1961: 116, pl. 21, fig. d; Orr, 1962: text fig. [radula], pl. 10, fig. B; Woodring, 1973: 477–478, pl. 74, figs. 4, 5; Abbott, 1974: 218, fig. 2399; Odé, 1983: 60, fig. 7; de Jong and Coomans, 1988: 82–83, pl. 38, fig. 450; Merlano and Hedegus, 1994: 187, fig. 710; Redfern, 2001: 93, pl. 43, fig. 395; Coltro, 2005: 1, pl. A, figs. 6, 7; Faber, 2007: 74, figs. 4, 5; Massemin *et al.*, 2009: 148 and text figures; Tunnell *et al.*, 2010: 214; Fraussen and Chino, 2011: 64; Daccarett and Bossio, 2011: 95, fig. 448; Zhang, 2011: 119, figs. 404(1–3); Landau and Vermeij, 2012: 122–127; Redfern, 2013: 144, figs. 414a,b.

Engina turbinella cruzana Nowell-Usticke, 1959: vi, 68–69; Warmke and Abbott, 1961: 116 [as a form].

Engina turbinella var. *cruzana* Nowell-Usticke, 1959: 68–69; Nowell-Usticke, 1969: 17, pl. 2, fig. “789” [790]; Boyko and Cordeiro, 2001: 61.

Description (based on 26 adult specimens): Largest adult specimen, 14.9 mm in length; smallest specimen, 6.6 mm in length. Spire occupies 30–50% of total length. Protoconch minute, of 1.5 smooth whorls, tan with or without a darker band. Protoconch almost always eroded away, very rarely remaining in adult specimens. Teleoconch of 5–6 whorls. Spiral sculpture consists of 6–10 (mode=8) primary spiral cords; the wide subsutural slope has secondary threads and usually a single primary (rarely two, rarely absent) cord somewhere between the suture and the mid-point of the subsutural slope; this cord may abruptly turn posteriorly at the edge of the varix. The periphery has 2–3 primary cords grouped over the axial nodes and microscopic threads; anteriorly there are 3–7 wide, rounded ribs widely separated by 3–5 secondary threads. Axial sculpture 8–13 (mode=10) elongated, undulating peripheral nodes on the final whorl, 9–14 (mode=10) on the penultimate whorl; usually prominent but less so on small specimens. Terminal varix slightly more developed than previous axial sculpture. Aperture small, constricted. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 3–7 (mode=5) denticles; the denticles are elongate but not lirate and do not project far into the aperture. The posterior-most two denticles are usually the most prominent and are fused; the anterior-most denticle forming a strong, long, thin rib that projects deep into the aperture and delimits the siphonal canal. Radial lirae (3–7, mode=4) at posterior end, usually long and thin but often not well-differentiated from columellar folds. Anterior to these are columellar folds (4–8, mode=6), irregular, some pustulose, some lirate, often limited to edge of parietal wall, anterior-most best-developed and forming a ridge on the interior of the columella. In some specimens, particularly small ones, the posterior half of the columella may be deeply excavated. Background color usually dark brown to black, rarely orange in some southeastern populations. Axial ribs at periphery always colored white, either as distinct spots or merged into a single spiral band; these white spots may be limited to the adapertural side of the ribs. Elsewhere, intersections of axial and spiral sculpture may or may not be present as white spots. 1° spiral cord on sub-sutural band may be white at termination. Aperture dark brown to black, fading to a lighter shade interiorly; outer lip denticles white, columellar ridge white. Operculum rounded, leaf-shaped, yellow with brown central radius. Radula figured by Orr (1962). Anatomy unknown.

Types: *Purpura turbinella* Kiener, 1836: Types not located at the Muséum d'histoire naturelle de la Ville de Genève (Y. Finet, pers. comm., 2011), the Muséum national d'Histoire naturelle, Paris (online database, 2011), nor the Natural History Museum UK (K. Way,

pers. comm., 2011), and are presumed lost. *Engina elegans* Gray, 1839: Syntypes, NHMUK 1982122 (5). The specimens are heavily worn and/or immature. *Engina zonata* Gray, 1839: Lectotype and paralectotype, NHMUK 1967592; the lectotype is the larger of the two, designated by Orr (1962). *Engina turbinella cruzana* Nowell-Usticke, 1959: Lectotype, AMNH 198494, designated by Boyko and Cordeiro (2001) [although listed as a variety on page 68 of Nowell-Usticke, 1959, the name was immediately used as a subspecies on the same page as well as earlier on page vi], additional specimens implied but their disposition is unknown except for UF 126216, Judith's Fancy, St. Croix, 7 paralectotypes.

Type Locality: *Purpura turbinella* Kiener, 1836: "Unknown." *Engina elegans* Gray, 1839, Atlantic Ocean. *Engina zonata* Gray, 1839: Atlantic Ocean. Lectotype label reads "West Indies." *Engina turbinella cruzana* Nowell-Usticke, 1959: West Coast [place name]. Judith's Fancy. Christiansted Harbor [all St. Croix]. Restricted by Boyko and Cordeiro (2001) to West Coast but paralectotypes at UF are from Judith's Fancy.

Other Material Examined (951 specimens): Florida: UF 12718 (1), S of Lake Worth Inlet, Palm Beach Co.; UF 126238 (1), Boynton Beach, Palm Beach Co.; MW (3), 18 m, Boynton Beach, Palm Beach Co.; UF 394034 (2), Hillsborough Light, Broward Co.; MW (2), 18 m, Pompano Beach, Broward Co.; UF 146654 (1), Miami, Miami-Dade Co.; UF 185179 (1), Bear Cut, Key Biscayne, Miami, Miami-Dade Co.; UF 126219 (4), Miami County Causeway, Miami-Dade Co.; UF 126227 (11), Biscayne Bay, Miami, Miami-Dade Co.; UF 238288 (3), Miami Beach, Miami-Dade Co.; UF 80978 (1), Key Largo, Monroe Co.; UF 239825 (1), Marathon, Key Largo, Monroe Co.; HGL (9), 3–4.5 m, Pickles Reef, Key Largo, Monroe Co.; UF 126223 (11), Little Molasses Reef, Key Largo, Monroe Co.; UF 80975 (2), Molasses Reef, Key Largo, Monroe Co.; UF 126228 (1), 4.0 km WSW of Carysfort Reef Light, Key Largo, Monroe Co.; UF 37855 (1), Dry Rocks, Key Largo, Monroe Co.; UF 123130 (51), UF 352066 (7), Looe Key, Big Pine Key, Monroe Co.; UF 352068 (6), UF 123056 (2), Little Torch Key, Monroe Co.; UF 61023 (4), UF 70396 (11), UF 192067 (3), Key West, Monroe Co.; UF 126218 (44), UF 126243 (92), UF 153382 (9), Middle Sambo Shoals, Key West, Monroe Co.; UF 80974 (41), Sambo Shoals, Key West, Monroe Co.; UF 126236 (3), Sand Key Light, Key West, Monroe Co.; UF 12714 (2), UF 70395 (3), UF 126231 (20), UF 192158 (2), MW (1), Pelican Shoals, Key West, Monroe Co.; UF 126222 (3), Washerwoman's Shoals, Key West, Monroe Co.; MW (7), 1.0–1.5 m, Sand Key, off Key West, Monroe Co.; UF 12717 (1), UF 126239 (13), Ft. Jefferson, Dry Tortugas, Monroe Co.; UF 12715 (1), Bush Key Reef, Dry Tortugas, Monroe Co.; UF 12716 (1), Garden Key, Dry Tortugas, Monroe Co. Bahamas: UF 126240 (5), North Bimini; GTW 4265a (1), tide pool, South Bimini; UF 126246 (10), Gun Cay, off Bimini; UF 80985 (1), Grand Bahama Island; UF

37853 (2), West End, Grand Bahama Island; UF 70391 (2), New Providence; UF 126224 (3), North Cay, Nassau, New Providence; UF 126226 (9), Delaport Point, New Providence; UF 126221 (2), Morgan's Bluff, Andros; UF 126234 (2), Frazier Hog Cay, Berry Islands; GTW 4265n (1), 1.0–2.5 m, Beachside, Chub Cay, Berry Islands; MW (2), Periwinkle Beach, Chub Cay, Berry Islands; HGL (1), Cat Island; HGL (2), Current, Eleuthera; MW (2), 18.0 m, Cay Sal. Cuba: UF 80982 (12), UF 80995 (5), Santiago; UF 80993 (5), Jauco; UF 80983 (7), Varadero; UF 80994 (1), Baracao; UF 54955 (1), Guantánamo; UF 80992 (4), Gibara; UF 17997 (6), La Habaña. Dominican Republic: UF 239824 (2), Barahona. Cayman Islands: UF 28935 (4), Preston Bay, Little Cayman; UF 239823 (1), Cayman Turtle Farm, Grand Cayman; UF 126230 (1), Red Bay, Grand Cayman. Jamaica: UF 61025 (4); UF 80987 (10), Flag Point. Puerto Rico: UF 80988 (1), Fajardo; GTW 4265z (1), 0.3–1 m, Escambron, San Juan; GTW 4265aa (3), 0.3–1 m, Enrique, La Parguera; GTW 4265ab (3), 0.3–1 m, Collao, La Parguera; GTW 4265ac (3), 0.3–1 m, Playa Buye, La Parguera; GTW 4265ad (7), 0.3–1 m, Media la Luna, La Parguera; GTW 4265ae (4), 1–3 m, El Corral, La Parguera; MW (3), Piñones Beach; HGL (7), Playa de Sardinera. U.S. Virgin Islands: UF 37856 (2), UF 80979 (43), Water Island; MW (3), 1 m, St. Croix; MW (1), 1 m, Ham Bay, St. Croix; UF 126216, St. Croix [7 paratypes of *Engina turbinella cruzana* (Nowell-Usticke, 1959)]. British Virgin Islands: UF 163643 (9), Tortola; KF 3929 (1), HGL (2), beached, Beef Island; HGL (3), 0.6 m, Buck Island; UF 163644 (4), Guana Island. Antigua: UF 80977 (3), UF 126235 (7); UF 120786 (2), Curtain Bluff; GTW 4265ai (5), 0.3–1 m, Long Bay; GTW 4265aj (2), 0.3–1 m, Deep Bay; GTW 4265ak (8), 0.3–1 m, Morris Bay; GTW 4265al (1), 0.3–1 m, Valley Church Bay; GTW 4265am (2), 0.3–1 m, Half Moon Bay; GTW 4265an (2), 0.3–1 m, Valley Church Bay; GTW 4265ao (1), 0.3–1 m, Cades Bay. Grenadines: EFG (1), 18 m, Montexuma Shoals, Mustique Island; KF 2503 (3), 12 m, St. Vincent, S end of Baliceaux Island; KF 5262 (3), 12 m, Savan Island; KF 2551 (1), 8–9 m, Cannoun Island. Grenada: GTW 4265t (12), GTW 4265u (14), GTW 4265v (8), GTW 4265w (4), GTW 4265x (7), GTW 4265y (2), 0.6–1.8 m, Coral Cove, Mt. Hartman Bay. Barbados: UF 80976 (2); UF 126220 (23), Hasting's Rock. Tobago: UF 70391 (3); UF 80980 (25); UF 126225 (6), UF 126237 (6), Buccoo Reef; UF 281378 (6), Friendship Beach; UF 281377 (7), UF 352067 (2), Scarborough; MW (2), Lambeau; MW (3), Irvine Bay. Mexico: EFG 26687 (1), 46–48 m, Campeche State, 22° 10.80' N, –91° 09.00' W; UF 383287 (4), Punta Hogna, Quintana Roo State; UF 264023 (1), Cayos Lobos, Quintana Roo State; UF 38338 (3), Cozumel, Quintana Roo State. Belize: GTW 4265c (4), 1 m, Sandbur Reef, Ambergris Caye; GTW 4265d (1), 1.5 m, Tres Cocos, Ambergris Caye; GTW 4265e (2), 0.3–1.5 m, Punta Robles, Ambergris Caye. Honduras: EFG 7365 (9), MW (2), Caribe Point, Isla Roatán; HGL (1), 0.5–1.3 m, Isla Roatán; GTW 4265g (1), 0.3–1.5 m, West Lime Key, SE Isla Roatán; GTW 4265h (1), GTW 4265i (2), GTW 4265j (1), 0.3–1.5 m,

Long Reef, Isla Roatán; GTW 4265k (6), SE Isla Roatán; GTW 4265l (1), 1–1.5 m, Old Port Royal, Isla Roatán; GTW 4265m (2), 1–1.5 m, Horseshoe Reef, Isla Roatán; HGL (5), Oak Ridge, Isla Roatán; KF 2173 (1), shallow water, Cayos Cochinos; KF 4141 (2), 2 m, Isla de Utila; MW (3), intertidal, Isla de Utila; HGL (19), Isla de Utila; UF 380423 (2), Guanaja; MW (2), 1 m, Guanaja. Costa Rica: UF 163876 (1), Punta Cahuita. Panama: UF 126217 (10), Colón; UF 80981 (9), UF 80989 (7), UF 160525 (2), Galeta Point; UF 80990 (2), Bocas del Toro; UF 160524 (3), Careening Cay, Bocas del Toro; UF 80991 (3), Devil's Beach; KF 3593 (2), Tiger Island; EFG 25590 (2), Isla Colón; UF 70393 (4), Bruja Point. Colombia: KF 3590 (3), Santa Marta; EFG 19507 (5), EFG 19508 (1), Isla de Providencia; EFG 25673 (1), Bocas del Toro. Venezuela: GTW 4265b (1), 7.3 m, Isla Morro Pelotas; GTW 4265ag (3), 2–5 m, Isla la Tortuga; HGL (5), Playa de Carenero; MW (1), Piedras Negras, Paraguaná Peninsula; MW (2), Isla de Margarita; MW (3), El Tunal, Isla de Margarita; EFG 19264 (1), Isla Borracha; KF 4735 (1), Punta San Juan. Netherlands Antilles: UF 80984 (2), UF 163642 (7), Bonaire; MW (6), 1.2 m, Kralendijk, Bonaire; UF 80986 (2), Aruba; UF 126245 (2), Palm Beach, Aruba. Brazil: GTW 4265af (1), 1–2 m, Buraco da Rachel, Fernando de Noronha; KF 78 (12), low tide, Fernando de Noronha.

Distribution: Widely distributed in southern Florida, rarely in the northern Gulf of Mexico, throughout the Bahamas, the Greater and Lesser Antilles, and along the Central American and northern South American coasts. Massemin et al. (2009) recorded this species from Îles du Salut, French Guiana. Daccarett and Bossio (2011) recorded it from most of the Colombian Caribbean coast. Perhaps the strangest aspect of this species' distribution is its occurrence on Fernando de Noronha, 2,400 km away from the next known site in French Guiana, where it co-occurs with *E. demani*. Tryon (1881) recorded *E. elegans* from Sierra Leone but it is not listed by Ardovalini and Cossignani (2004) and this record is probably in error.

Habitat: A shallow water species found from the intertidal zone to ca. 20 m. It seems to occur in deeper water off Florida and the northern Gulf of Mexico than elsewhere in the Caribbean. It is most commonly found under slabs of coral rubble, often in pairs, often almost completely covered in a thick, coralline algal deposit.

Variation in Specimens: Specimens vary greatly in size and degree of "fusiformity," but are relatively uniform in sculpture and, with few exceptions, coloration. All specimens have a peripheral band of white spots on the axial cords that may merge into a single unbroken band. In some populations the single spiral cord on the sub-sutural plane and/or the spiral cords anterior to the periphery may have white nodes as well. The two posterior-most outer lip denticles are almost always fused into a single large tooth. In the southeastern populations some specimens are an orange color (see discussion below) with numerous white spots. Specimens from the

Bahamas and the Lesser Antilles tend to be smaller than elsewhere, but there are numerous exceptions.

Etymology: *Engina turbinella* (Kiener, 1836): Latin, diminutive of *turbina*, a top. *Engina elegans* Gray, 1839: Latin, elegant. *Engina zonata* Gray, 1839: Latin, banded. *Engina turbinella cruzana* Nowell-Usticke, 1959: Spanish, *cruz* (cross), from the original name given by Christopher Columbus to the island of St. Croix, Santa Cruz.

Comparison with Other Species: The combination of a uniformly dark background color with white spots or bands, fused outer lip teeth, and dark aperture with white teeth characterize this species. Some specimens are similar to the Brazilian *E. permixta*; that is a relatively larger species with fewer axial ribs on both the final whorl (8–13 in *E. turbinella*, 7–10 in *E. permixta*) and the penultimate whorl (9–14 in *E. turbinella*, 8–10 in *E. permixta*). *Engina turbinella* never shows the wide range of colors seen in *E. permixta*. See Table 1 for a comparison with other species.

Discussion: *Engina turbinella* (Kiener, 1836) is a widespread and usually shallow water species occurring throughout much of the tropical western Atlantic Ocean. It is a baffling species varying greatly in size, shape, and coloration. Three color forms are apparent, all named, that appear rather distinct unless a large number of specimens is studied. These are discussed below.

Purpura turbinella Kiener, 1836. Louis Charles Kiener curated the vast (150,000 specimens) collection of Baron Jules Paul Benjamin Delessert, describing and illustrating many species in his *Spécies Général* (Dance, 1966). This included the "*jolie petite espèce*" *Purpura turbinella* from an unknown habitat, originally from the Prince Masséna collection, which Delessert had acquired in 1840. Subsequently this name has been almost universally applied to all western Atlantic Ocean *Engina* taxa as "*Engina turbinella*." Although the type is apparently lost, the illustrations (Figure 69) clearly show an orange shell with small white nodules above and below the usual peripheral row of nodules. This is not the widely distributed typical form illustrated in most accounts as *Engina turbinella*. Kiener's illustrations match our specimens from Scarborough, Tobago (Figures 70, 71). Although the size of the figured type specimen - "7 lig[nes]" [= 15.8 mm] is larger than the largest specimen we have seen from there (12.3 mm), given the great variation in size among other Caribbean *Engina* species we do not feel this is significant. These specimens represent a morph that appears to have a rather limited distribution from Barbados and Tobago to adjacent western Venezuela, including the Netherlands Antilles. It should be noted that orange shells occasionally are seen throughout the remainder of the western Atlantic Ocean and that shells may fade to an orange or tan color as well.

Engina zonata Gray, 1839. Tomlin (1928) mentioned a tablet at NHMUK labeled "*Enzina* [sic] *zonata* Gray. B.V. 113" with two examples. He misidentified them as *Engina leucozona* (Philippi, 1844) from the Mediterranean Sea.

Orr (1962) quoted Tomlin as saying the specimens represent "a possible type lot" but this phrase does not appear in his 1928 paper. Bartsch (1931) did not pick a lectotype of *zonata*, but simply illustrated one of the two specimens as the genotype of *Engina* without further comment. Orr (1962) selected and illustrated a lectotype from the same lot that Tomlin saw. Gray (1839) greatly mis-represented the size of the specimen as 1.5 inches long, a fact apparently overlooked by Bartsch (1931) but noted by Orr (1962). Tryon (1883: 196) also commented on *Engina zonata*: "This is also a lost species." But types exist and prove to be *E. turbinella*. This is the morph most commonly found throughout the western Atlantic, where it insensibly grades into the other *E. turbinella* morphs described here. It is often quite large, particularly in populations off Miami and Panamá. Like the *E. turbinella* morph described above it usually has small, white nodules below the periphery (not apparent on the lectotype but visible on the paralectotype of *E. zonata*) but lacks the white sub-sutural nodules.

Engina elegans Gray, 1839 (and *Engina turbinella cruzana* Nowell-Usticke, 1959). This is the morph usually associated with the Greater Antilles and the Bahamas. It is often quite small in comparison to the *E. zonata* morph and usually lacks the sub-peripheral white nodules.

Examination of over 900 specimens indicates that these three morphs seem to blend from one to the other without clear-cut distinctions. Thus we prefer to recognize only the single species, *E. turbinella*. However, phylogenetic work may yet separate this "species" into two or more potentially cryptic species. The southeastern Caribbean form, the basis of the name *Purpura turbinella* Kiener, 1836, in particular seems the most morphologically and zoogeographically distinct of the three morphs. A peculiar form from the Grenadines (Figure 101) may represent a distinct species as well.

This is the only extant *Engina* species from the western Atlantic with a fossil record. It was recognized from the middle Miocene of Panamá by Woodring (1973) and the late Pleistocene of the Dominican Republic by Landau and Vermeij (2012).

***Engina williamsae* new species (Figures 13, 103–107)**

Description (based on 11 adult specimens): Largest specimen, 15.0 mm in length; smallest specimen, 11.5 mm in length; holotype 12.6 in length \times 7.4 mm in width. Spire occupies 60% of total length. Protoconch minute, of 1.5 smooth whorls, white with tan patches or bands. Teleoconch of ca. 5 whorls. Spiral sculpture consists of a wide subsutural slope with a narrow primary thread with microscopic secondary threads; the periphery has 4 indistinct primary cords over the axial nodes and microscopic threads; anteriorly there are 5 wide, flat primary cords separated by deeply incised channels. Axial sculpture of numerous microscopic threads on sub-sutural band and 8–10 (mode=9) elongated primary peripheral nodes on the final whorl, 9–10 (mode=9) on

penultimate whorl. Terminal varix only slightly more developed than previous axial sculpture. Aperture small, constricted. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 5–6 (mode=5) semi-lirate denticles, the anterior-most forming a weak, long, thin rib that projects deep into the aperture and delimits the siphonal canal, barely perceptible in some specimens. Radial lirae (2–5, mode=5) at posterior end, weak and irregular. Anterior to these are columellar folds (2–6, mode=6), weak or absent from center of columella, often limited to edge of parietal wall, anterior-most two best-developed and forming a ridge on the interior of the columella. Background color white, subsutural slope gray, wide brown blotches on the subsutural slope and between the axial ribs on the posterior half, leaving a white sub-peripheral band, anteriorly colored with brown spots, more or less aligned axially. Aperture pale tan. Operculum rounded, leaf-shaped, yellow with brown central radius. Radula and anatomy unknown.

Holotype: UF 478947 (ex MW).

Type Locality: 15 m, off Egmont Key, Hillsborough Co., Florida, USA.

Paratype(s): UF 478946 (1), 15 m, off Egmont Key, Hillsborough Co., Florida, USA (ex MW); BMSM 75998 (1), off Egmont Key, Hillsborough Co., Florida, USA (ex MW).

Other Material Examined (9 specimens): Western Florida: UF 239809 (1), 220 m, off Egmont Key, Hillsborough Co.; HGL (2), MW (4), 15 m, off Egmont Key, Hillsborough Co.; MW (1), 14 m, off Egmont Key, Hillsborough Co.; MW (1), 14 m, off Anna Maria Island, Manatee Co.

Distribution: Known only from off Egmont Key and adjacent Anna Maria Island, Hillsborough and Manatee counties, Florida, Gulf of Mexico.

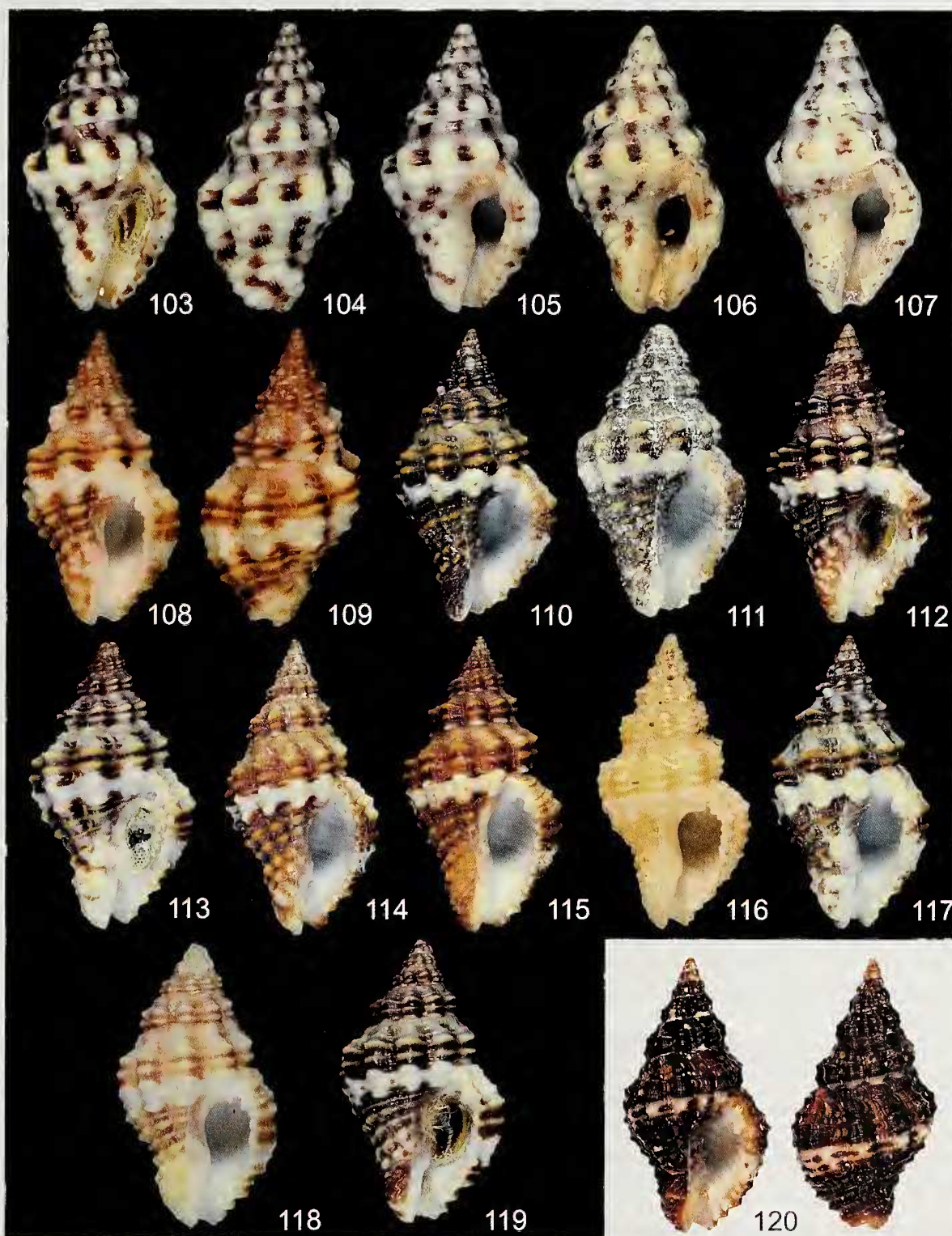
Habitat: Live and dead specimens collected on rock reef in 15 m. Other specimens known to 220 m.

Variation in Specimens: The few known specimens are remarkably uniform in coloration and sculpture.

Etymology: Named for Margaret "Peggy" Williams of Tallavast, Florida, who collected most of the known examples.

Comparison with Other Species: This species is similar to *E. corinnae*. That species has more prominent spiral sculpture over the entire shell, including the sub-sutural band, which is nearly smooth in *E. williamsae*. See Table 1 for a comparison with other species.

Discussion: *Engina williamsae* is only known from Egmont Key and Anna Maria Island off the Gulf coast of Florida. These sites are at the mouth of Tampa Bay, a large open-water estuary. It has not yet been found on



Figures 103–120. *Engina* species. **103–107.** *Engina williamsae* new species. **103–104.** Holotype, UF 478947, 14.5 mm. **105.** Paratype, BMSM 75998, 13.0 mm. **106.** Paratype, UF 479946, 15.0 mm. **107.** MW, 13.6 mm. All specimens from 15 m, off Egnont Key, Hillsborough Co., Florida. **108–109.** *Hesperisternia karinae* (Nowell-Usticke, 1959). **108–109.** Holotype, AMNH 193771, 23 mm. **110.** KF 2505, 5–7 m, Ronde Island, Grenada, 18.5 mm. **111.** HGL, 9.1 m, Pickles Reef, Monroe Co., Florida, 19.9 mm. **112.** HGL, 201 m, St. Anne, Guadeloupe, 19.8 mm. **113.** GTW 6613c, 20–25 m, off Guarapari, Espírito Santo State, Brazil, 21.0 mm. **114.** GTW 6613a, 6.1 m, Tambor Cay, Panamá, 18.5 mm. **115.** GTW 6613e, French Guiana, 17.1 mm. **116.** GTW 6613b, 12 m, off Guarapari, Espírito Santo State, Brazil, 21.9 mm. **117.** KF 4535, Isla Los Aves, Venezuela, 19.3 mm. **118.** HGL, Playa de Ponce, Puerto Rico, 21.1 mm. **119.** KF 2947, Port Louis, Guadeloupe, 20.8 mm. **120.** *Hesperisternia* sp., GTW 6613d, Amuay, Venezuela, 18.8 mm.

adjacent Mullet and Sister keys. Given the amount of recreational shelling that takes place in the area it is surprising that more examples have not been found. Most specimens are worn and crabbed.

Hesperisternia Gardner, 1944

Type Species: *Hesperisternia waltonia* Gardner, 1944, by original designation.

Discussion: In *Hesperisternia* the lirae extend much further back within the aperture than in *Engina*. Vermeij (2006) reviewed the fossil and Recent species. Additional notes are given here for *Hesperisternia karinae* (Nowell-Usticke, 1959) because it occupies a much larger range than is usually thought and is often misidentified in collections. It is redescribed and its distribution is given so that its proper place in the western Atlantic fauna may become more clear.

In addition to *H. karinae*, other western Atlantic Ocean Recent taxa include *Hesperisternia multangula* (Philippi, 1848) and *Hesperisternia harasewychi* (Petuch, 1987). Abbott (1986) named a subspecies, *H. multangula grandana*, which Vermeij (2006) considered a minor variant, but which Petuch (2013) raised to a full species. *Hesperisternia itzamnai* Watters, 2009, and *Engina janowskyi*, placed in *Hesperisternia* by Watters (2009), are reallocated to *Engina* based on the study of Landau and Vermeij (2012). An additional undescribed *Hesperisternia* occurs at Amuay, Venezuela, but it is only known to us from a single specimen (Figure 120).

Hesperisternia karinae (Nowell-Usticke, 1959) (Figures 68, 108–119)

Tritonidea orbignyi Payraudeau, 1826. Dall and Simpson, 1901: 400 [misidentification].

Cantharus karinae Nowell-Usticke, 1959: 69, pl. 4, fig. 4; Warmke and Abbott, 1961: 118 [in synonymy of *Cantharus lautus* Reeve, 1846]; Nowell-Usticke, 1969: 17, pl. 4, fig. 4; Nowell-Usticke, 1971: 13–14, pl. 2; Leal, 1991: 153, pl. 19, fig. G.

non *Cantharus lautus* Reeve, 1846. — Warmke and Abbott, 1961: 118, pl. 21, fig. c [misidentification].

Pisania karinae (Nowell-Usticke, 1959). — Kaicher, 1986: card 4370; de Jong and Coomans, 1988: 84.

Hesperisternia karinae (Nowell-Usticke, 1969 [sic]). — Vermeij, 2006: 81.

Hesperisternia karinae (Nowell-Usticke, 1953 [sic]). — Watters, 2009: 271.

Description (based on 19 adult specimens): Largest adult specimen, 25.0 mm in length; smallest specimen, 17.0 mm in length. Spire occupies 50% of total length. Protoconch minute, of 1.5 smooth whorls, tan with a brown band. Teleoconch of ca. 6.25 whorls. Spiral sculpture of 10–13 (mode = 12) primary ribs, usually absent from the sub-sutural ramp, between which are single secondary threads flanked by a few tertiary threads. Axial sculpture of large primary ribs, absent or

greatly reduced on the subsutural slope, most developed at the periphery; 6–8 (mode = 7) on both the last whorl and on the penultimate whorl. Intersections of axial and spiral sculpture form elongated spiral pustules on the primary spiral cords. Terminal varix only slightly more developed than previous axial sculpture. Aperture oval, constricted. Anal canal bounded by single parietal denticle on columella and single anal denticle on outer lip. Outer lip with 8–10 (mode = 10) lirae denticles, in all but the anterior two, which are quite short, the lirae curve back deep into the aperture. The long, thin rib that projects deep into the aperture and delimits the siphonal canal in some *Engina* is not present. Radial lirae at posterior end composed of combinations of 4–10 pustules and irregular lirae, often mixed together. Anterior to these are columellar folds (8–10, mode = 10) posteriorly composed of irregular pustules, anterior 2–3 folds of long lirae. Interior ledge of columella well-developed. Background color yellow or tan with a prominent, wide, undulating, white peripheral band. This band is often bounded on each side by a thin dark brown line and may have dark brown flecks embedded within it. A diffuse, broad, dark band occurs above and below the white peripheral band. Subsutural slope and pustules lighter in color – yellow or tan. Aperture white, columella showing through to brown below. Operculum rounded, leaf-shaped, yellow with brown central radius. Radula and anatomy unknown. Leal (1991) figured the protoconch.

Holotype: AMNH 193771.

Type Locality: N of Fredericksted, [St. Croix, US Virgin Islands].

Paratype(s): AMNH 294356 (1); UF 154704 (1); both from the type locality.

Other Material Examined (35 specimens): Florida: UF 352842 (1), UF 352843 (1), dredged off Delray Beach, Palm Beach Co.; UF 126511 (1), 27 m, off Palm Beach Inlet, Palm Beach Co.; UF 126510 (1), 37 m, off Palm Beach, Palm Beach Co.; UF 157523 (4), 18 m, Pompano Beach, Broward Co.; UF 398301 (1), 365.8 m, off Hillsboro, Broward Co.; HGL (1), 9 m, off Pickles Reef, Key Largo, Monroe Co. Bahamas: UF 168507 (1), Cat Cay, Bimini. Puerto Rico: UF 162628 (1), Córcega Beach, Rincón; UF 162629 (1), Rincón; HGL (3), Playa de Ponce. U.S. Virgin Islands: UF 154704 (1), N of Fredericksted, St. Croix [paratype]. Guadeloupe: HGL (3), 201 m, St. Anne; KF 2947 (4), Port Louis. Grenada: KF 2505 (1), 5–7 m, Ronde Island. Panama: GTW 6613a (1), 6 m, Tambor Cay. Venezuela: KF 4535 (1), Isla Los Aves. French Guiana: GTW 6613e (1). Brazil: HGL (1), 6 m, Salvador, Bahia State; HGL (1), 10–12 m, Salvador, Bahia State; HGL (1), off Guarapari, Espírito Santo State; GTW 6613c (2), 20–25 m, off Guarapari, Espírito Santo State; GTW 6613b (2), 12 m, off Guarapari, Espírito Santo State.

Distribution: This is a rare but widely distributed species: southeastern Florida, sporadically throughout the eastern Caribbean to Espírito Santo State, Brazil, but with considerable gaps in this distribution. It has not been recorded from Central America beyond Panamá, or from Cuba or Hispaniola, although it probably occurs there. It was not included as part of the North American fauna by Abbott (1974). Recorded by Dall and Simpson (1901) from Ponce and Culebra, Puerto Rico, as *Tritonidea orbigny* Payraudeau, 1826. Nowell-Usticke (1971) added Antigua, Barbados, Grenada, Curaçao, and Aruba to his original description. Leal (1991) recorded it from Trindade and Vitória seamounts.

Habitat: Live and dead individuals have been found from 6–366 m. It appears to live in shallower water in the southern Caribbean than in the northern part of its range. It has been found on calcareous rubble.

Variation in Specimens: The degree of development of the axial sculpture varies considerably. The overall coloration varies from yellowish to a mahogany color but the wide, white peripheral band is always present.

Etymology: Named after Nowell-Usticke's wife, Karin.

Comparison with Other Species: This relatively large and brightly colored species should not be confused with any other species from the western Atlantic. No species of *Engina* from there has a similar color pattern, or the elongate, lirate outer lip denticles, or the pustulose radial lirae. See Table 1 for a comparison with other species.

Discussion: This species has been identified in most collections as *Buccinum lautum* Reeve, 1846, described from an unknown locality. That species is the eastern Pacific taxon *Gemophos lautus* (Reeve, 1846).

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LITERATURE CITED

- Abbott, R.T. 1974. American Seashells. 2nd ed. Van Nostrand Reinhold Co., New York City, 663 pp., 24 pls.
 Ardovini, R. and T. Cossignani. 2004. West African Seashells. L'Informatore Piceno, Ancona, 319 pp.

- Boyko, C.B. and J.R. Cordeiro. 2001. Catalog of Recent type specimens in the Division of Invertebrate Zoology, American Museum of Natural History. 5, Mollusca, part 2 (Class Gastropoda (exclusive of Opisthobranchia and Pulmonata), with supplements to Gastropoda (Opisthobranchia) and Bivalvia). Bulletin of the American Museum of Natural History (262): 170 pp.
 Cernohorsky, W.O. 1975. Supplementary notes on the taxonomy of buccinid species of the subfamily Pisaninae (Mollusca: Gastropoda). Records of the Auckland Institute and Museum 12: 175–211.
 Coltro, J. 2005. Three new Buccinidae (Mollusca: Gastropoda) from Brasil. Strombus 12: 1–6.
 Crovo, M.E. 1971. A new *Engina* in Florida. Veliger 14: 30, figs. 1–3.
 Daccarett, E.Y. and V.S. Bossio. 2011. Colombian Seashells from the Caribbean Sea. L'Informatore Piceno, Ancona. 384 pp.
 Dall, W.H. and C.T. Simpson. 1901. The Mollusca of Porto Rico. U. S. Fisheries Commission Bulletin 20: 351–524, pls. 53–58.
 Dance, S.P. 1966. Shell Collecting. University of California Press, Berkeley, 344 pp., 25 pls.
 Dornellas, A.P.S. and L.R. Simone. 2011. Annotated list of type specimens of mollusks deposited in Museu de Zoologia da Universidade de São Paulo, Brasil. Arquivos de Zoologia 42(1): 1–81.
 Duclos, P.L. 1840. Histoire naturelle générale et particulière de tous les genres de coquilles univalves marines à l'état vivant et fossile publiée par monographie. Genre *Columbella*. Didot, Paris, 1 pp., 13 pls.
 Dunker, W. 1860. Neue japanische Mollusken. Malazozoologische Blätter für 1859: 221–224.
 Eston, V.R., A.E. Migotto, E.C. Oliveira-Filho, S.A. Rodrigues, and J.C. Freitas. 1986. Vertical distribution of benthic marine organisms on rocky coasts of the Fernando de Noronha Archipelago (Brasil). Boletim do Instituto Oceanográfico 34: 37–53.
 Faber, M.J. 2007. Marine gastropods from the ABC-islands and other localities. 18. The genus *Engina* Gray, 1839 (Gastropoda: Buccinidae). Miscellanea Malacologica 2(4): 73–77.
 Fraussen, K. and M. Chino. 2011. Notes about *Engina* J.E. Gray, 1839 (Gastropoda: Buccinidae) with description of three new species from the West Pacific. Visaya 3(3): 63–75.
 Gray, J.E. 1839. Molluscos animals, and their shells. In: The zoology of Captain Beechey's voyage, comp. from the collections and notes made by Captain Beechey, the officers and naturalist of the expedition, during a voyage to the Pacific and Behring's Straits performed in His Majesty's ship *Blossom*, under the command of Captain F. W. Beechey ... in the years 1825, 26, 27 and 28, by J. Richardson ... N. A. Vigors ... G. T. Lay ... E. T. Bennett ... Richard Owen ... John E. Gray ... Rev. W. Buckland ... and G. B. Sowerby ... Illustrated with upwards of fifty finely coloured plates by Sowerby. Pub. under the authority of the lords commissioners of the Admiralty. H.G. Bohn, London, pp. 101–143.
 Gray, J.E. 1847. A list of the genera of Recent Mollusca, their synonyma and types. Proceedings of the Zoological Society of London 15: 129–219.
 Houart, R. 1994. Illustrated Catalogue of Recent Species of Muricidae named since 1971. Verlag Christa Hemmen, Wiesbaden. 178 pp., 29 pls.

- de Jong, K.M. and H.E. Coomans. 1988. Marine Gastropods from Curaçao, Aruba and Bonaire. E.J. Brill, Leiden, 261 pp., 47 pls.
- Kaicher, S.D. 1986. Buccinidae part 2 (Pack #44). S.D. Kaicher.
- Keen, A.M. 1971. Seashells of Tropical West America. 2nd ed. Stanford University Press, Stanford, 1064 pp.
- Kempf, M. and H.R. Matthews. 1968. Marine mollusks from north and northeast Brasil. I – Preliminary list. Arquivos da Estação de Biologia Marinha da Universidade Federal de Ceará 8: 87–94.
- Kiener, L.C. 1836. Genre Pourpre. Spécies général et iconographie des eoquilles vivantes comprenant la collection du Muséum d'histoire naturelle de Paris la collection Lamarck, eelle du prince Masséna (appartenant maintenant a M.B. Delessert) et les découvertes récentes des voyageurs par L.C. Kiener ... continué par ... P. Fischer. Vol. 8. J. Baillière, Paris. 151 pp., 46 pls.
- Küster, H.C. 1858. Die Gattungen *Buccinum*, *Purpura*, *Concholepas* und *Monoceros*. [In:] Schubert G. H. and Wagner, A., 1858–1860. Systematisches Conchylien-Cabinet von Martini und Chemnitz. Band 3, Abtheilung 1, 229 pp.
- Lamarck, J.P.B.A. de Monet de. 1822. Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie. Tome septième. Paris, 3 + 711 pp.
- Landau, B. and G.J. Vermeij. 2012. The genera *Engina* and *Ameranna* nov. gen. (Mollusca: Gastropoda, Buccinoidea, Buccinidae, Pisaninae) from the Western Atlantic Neogene. *Cainozoic Research* 9(1): 121–133.
- Leal, J.H. 1991. Marine Prosobranch Gastropods from Oceanic Islands off Brazil. Dr. W. Backhuys/Universal Book Services, Oegstgeest, 418 pp.
- Lee, H.G.L. 2009. Marine Shells of Northeast Florida. Jacksonville Shell Club, Inc. 204 pp., 795 figs.
- Linnaeus, C. 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus 1. Editio decima, reformata. Salvius, Holmiæ, 4 + 824 pp.
- Lister, M. 1685–1692. *Historiae conchyliorum*. Londini, aere incisi, sumptibus authoris.
- Lopes, H.S. and M. Alvarenga. 1955. Contribuição ao conhecimento dos moluscos da ilha Fernando de Noronha – Brasil. *Boletim do Instituto Oceanográfico* 6: 157–190.
- Massemin, D., Lamy, D., Pointier, J-P. and O. Gargominy. 2009. Coquillages et escargots de Guyane. Biotope, Mèze (Collection Parthénopé), Muséum national d'Histoire naturelle, Paris, 456 pp.
- Matthews, H.R. and M. Kempf. 1970. Moluscos marinhos do norte e nordeste do Brasil. II. Moluscos do Arquipélago de Fernando de Noronha (com algumas referências ao Atol das Rocas). *Arquivos de Ciências do Mar* 10: 1–53.
- Melville, J.C. 1893. Descriptions of twenty-five new species of marine shells from Bombay. Collected by Alexander Abercrombie, Esq. *Memoires and Proceedings of the Manchester Literary & Philosophical Society*, series 4, 7(1): 52–66.
- Melville, J.C. 1894a. Description of a new species of *Engina* from the Loyalty Islands. *Proceedings of the Malacological Society of London* 1: 51.
- Melville, J.C. 1894b. Description of a new species of *Engina* (*E. epidromidea*) from Bombay. *Proceedings of the Malacological Society of London* 1: 162.
- Melville, J.C. 1895. Descriptions of four new species of *Engina* and a new species of *Defrancia*. *Proceedings of the Malacological Society of London* 1: 226–228.
- Melville, J.C. and R. Standen. 1895. Notes on a collection of shells from Lifu and Uvea, Loyalty Islands, formed by the Rev. James and Mrs. Hadfield, with list of species. *Journal of Conchology* 8: 84–132.
- Nowell-Usticke, G.W. 1959. A Check List of the Marine Shells of St. Croix, U.S. Virgin Islands. Lane Press, Burlington, 90 pp.
- Nowell-Usticke, G.W. 1969. A Supplementary Listing of New Shells (illustrated) to be added to the Check List of the Marine Shells of St. Croix. Privately published. 32 pp., 6 pls.
- Nowell-Usticke, G.W. 1971. A Supplementary Listing of New Shells (illustrated) Revised Edition to be added to the Check List of the Marine Shells of St. Croix. Privately published. 32 pp., 6 pls.
- Odé, H. 1983. Distribution and records of the marine Mollusca in the northwest Gulf of Mexico. *Texas Conchologist* 19: 54–63.
- Pace, S. 1902. Contributions to the study of the Columbelloidea. *Proceedings of the Malacological Society of London* 5: 36–154.
- Pease, W.H. 1860. Descriptions of new species of Mollusca from the Sandwich Islands. *Proceedings of the Zoological Society of London*, part 27: 141–148.
- Petuch, E.J. 2013. Biogeography and Biodiversity of Western Atlantic mollusks. CRC Press, Boca Raton. 234 pp., text figures.
- Redfern, C. 2001. Bahamian Seashells. Bahamianseashells.com, Inc., Boca Raton, Florida, 280 pp., 124 pls.
- Redfern, C. 2013. Bahamian Seashells. Bahamianseashells.com, Inc., Boca Raton, FL. 501 pp., 1161 figs.
- Reeve, L.A. 1846. Monograph of the genus *Ricnula*. *Conchologia Iconica* 3. London, pls. 1–6.
- Rios, E.C. 1975. Brazilian Marine Mollusks Iconography. Fundação Universidade do Rio Grande Centro de Ciências do Mar Museu Oceanográfico. 331 pp, 91 pls.
- Smith, E.A. 1884. Mollusca. [In:] Report of the zoological collections made in the Indo-Pacific Ocean during the voyage of H.M.S. "Alert", 1881–82. *Proceedings of the Zoological Society of London* for 1884: 34–116, 487–508.
- Sowerby, G.B. 1832. Characters of new species of Mollusca and Conchifera, collected by Mr. Cuning: Genus *Columbella*. *Proceedings of the Committee of Science and Correspondance of the Zoological Society of London*, part II, Taylor, London: 113–120.
- Tomlin, J.R. le B. 1928. On *Engina zonata* of Gray and of Reeve. *Nautilus* 42: 40.
- Tryon, G.W. 1881. Manual of Conchology. Vol. III. Tritonidae, Fusidae, Buccinidae, privately printed, Philadelphia. Pt. 10. pp. 65–128.
- Tryon, G.W. 1883. Manual of Conchology. V. Marginellidae, Olividae, Columbelloidea. Privately printed, Philadelphia, 276 pp, 62 pls.
- Tunnell, J.W., Andrews, J., Barrera, N.C. and F. Moretzsohn. 2010. Encyclopedia of Texas Seashells. Texas A and M Press, College Station. 512 pp.

- Van Osselaer, C. 1999. Counting shell whorls. Remarks. *Apex* 14: 33–42.
- Vermeij, G.J. 2006. The *Cantharus* group of pisiniine buccinid gastropods: review of the Oligocene to Recent genera and description of some new species of *Gemophos* and *Hesperisternia*. *Cainozoic Research* 4: 71–96, 27 figs.
- Warmke, G.L. and R.T. Abbott. 1961. Caribbean Seashells. Livingston Publishing Company, Wynnewood, 348 pp., 44 pls.
- Watters, G.T. 2009. A revision of the western Atlantic Ocean genera *Anna*, *Antillophos*, *Bailya*, *Caducifer*, *Monostiolum*, and *Parviphos*, with description of a new genus, *Dianthiphos*, and notes on *Engina* and *Hesperisternia* (Gastropoda: Buccinidae: Pisaniinae) and *Cumia* (Colubrariidae). *The Nautilus* 123: 225–275.
- Wood, W. 1828. *Index Testaceologicus; or, a Catalogue of Shells, British and Foreign, arranged according to the Linnean System; with the Latin and English Names, References to Authors, and Places where found. Illustrated with 2300 figures. Second edition, corrected and revised. Supplement.* Wood, London, 2 + 59 pp, 38 pls.
- Woodring, W.P. 1973. Geology and paleontology of Canal Zone and adjoining parts of Panama: description of Tertiary mollusks (additions to gastropods, scaphopods, pelecypods: Nuculidae to Malleidae). U.S. Geological Survey Professional Paper 306-E: 453–539, 82 pls.
- Zhang, Deng Yan. 2011. *Antiguan Shallow-water Seashells.* MdM Publishing, Wellington, FL. 210 pp.